

# A revision of the English Wealden Flora, II. Equisetales

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**SYNOPSIS.** The three known equisetalean species from the English Wealden are revised and type specimens selected. Their geological occurrence and stratigraphical range are discussed.

*Equisetum burchardtii* Dunker is known only from *in situ* rhizomes and tubers in the English Wealden, but in the German Wealden also from subterranean parts of aerial shoots. An emended diagnosis is given, a neotype chosen and a reconstruction suggested. The poorly characterized tuberous species *Equisetites yokoyamae* Seward is discussed, compared with other tuberous material and the lectotype selected. Both species were probably deciduous. *Equisetites lyellii* (Mantell) Seward, which occurs extensively *in situ* in the soil beds of the Wealden in Sussex, is known also from dispersed acrial parts in fragment partings above the soil beds. The diagnosis is emended to include cuticular and anatomical details and the lectotype is chosen. *E. lyellii* was probably winter-green. The subgeneric affinities of the fossil species are discussed in relation to comparable extant species.

*Pilasporites allenii* Batten, the probable spore of *E. lyellii* which is now known from dispersed sporangiophore heads, is discussed and compared to other putative equisetalean spores. Palaeoenvironments are considered and probable habitats suggested.

## INTRODUCTION

Many beds in the Wealden succession of south-east England contain plant roots in positions of growth. Usually the tops of the plants have been eroded away and it is normally impossible to suggest affinities for such isolated roots, although occasionally it is reasonable to guess that they belonged to *Equisetum* or *Equisetites*. However, sometimes they are connected to excellently preserved equisetalean rhizomes, tubers and underground parts of aerial shoots, and can then be identified with confidence. Three members of the Equisetales have been described from the English Wealden: *Equisetum burchardtii* Dunker, *Equisetites yokoyamae* Seward and

*Equisetites lyellii* (Mantell) Seward. From England *E. burchardtii* is known only as lengths of thin rhizomes bearing tubers, but since aerial shoots are known from the Wealden of Germany these are described and figured here. *E. yokoyamae* is very poorly characterized and may even represent only a different preservational state of *E. burchardtii*. *E. lyellii* is by far the best represented of the three species, known from an abundance of excellent material found in positions of growth and is one of the few Wealden plant species which can still reliably be found in the field. It is widely preserved *in situ* in the 'soil beds' (fossil aquatic soils of Allen, 1976) in the Wealden succession of south-east England and the bulk of this paper is devoted to the taxonomy and geological significance of this species.

The material studied belongs to several collections made by

a number of people over a period of about 150 years, starting with Mantell (1833) and later Rufford (Seward 1894), but notably in this century by Allen (1941, 1947, 1976) and most recently by Batten. The collections are mainly housed in the British Museum (Natural History) (B.M.(N.H.)) with numbers prefixed V.; the Sedgwick Museum, Cambridge with numbers prefixed K.; the Museum für Naturkunde, Humboldt University, East Berlin, numbers without a prefix. The Appendix lists all the specimens figured here together with their locality, stratigraphical horizon and present location, as well as details of other interesting specimens which have not been figured.

## GEOLOGICAL OCCURRENCE

Of the several Wealden formations the Wadhurst Clay, which is thought to be of Valanginian age, has yielded the most numerous *Equisetum* and *Equisetites* finds both in positions of growth and as dispersed fragments. Most of the 'soil beds' are in the Wadhurst Clay and the majority of the specimens in them are referable to *E. lyellii* without reservation. Conveniently referred to as 'soil beds' for descriptive purposes, they were undoubtedly aquatic (Allen 1976) and are discussed in more detail below. Allen (1976, Appendix I) has given a comprehensive check-list of soil horizons and their localities in the Wealden of the Weald. Details of the upper parts of the aerial shoots of the species have been obtained entirely from macroscopic stem fragments which are common in thin debris partings associated with the soil beds. Older and younger occurrences of the species are scarce, but dispersed remains of aerial stems have been found in Berriasian and Valanginian-?Hauterivian strata in the Weald. Some of the *in situ* *Equisetum* which has been recorded from these rocks may differ from *E. lyellii*. In particular some rhizomes are very slender; not so slender, however, as the tuber-bearing rhizomes of *E. burchardtii*. Tuberos forms of *Equisetum*, including *E. burchardtii*, are rare and, by contrast with *E. lyellii*, have not been found in the Wadhurst Clay Formation. Records so far are limited to isolated occurrences in arenaceous facies of the Ashdown Beds Formation and Weald Clay Group (Allen 1959, 1962, 1976; Kennedy & MacDougall 1969). It is clear that *E. lyellii* can have rather thin rhizomes, such as those shown in Fig. 17 from Poundsford (top Purbeck) and in Fig. 23 from the Brede Soil Bed (Wadhurst Clay). They could represent a response to less suitable environmental conditions such as an increase in salinity or more arenaceous deposition. Similar specimens from Philpots Quarry (lower Grinstead Clay) and the Hackenden Soil Bed (possibly the same horizon) are less well preserved, but can be identified with confidence as *E. lyellii* on the basis of their characteristically very short internodes. However, the possible presence of one or more completely different and as yet unrecognized species should not be ruled out because preservation is often so poor as to preclude specific identification.

Many other beds contain roots in position of growth but the plants to which they belonged are usually missing because an erosion surface supervenes. It is normally impossible therefore to suggest affinities for them, although when interbedded with deposits in which rhizomes of *Equisetum* or *Equisetites* occur, it is reasonable to guess that they too are equisetalean.

All the equisetalean material described from the Wealden

of Germany by Dunker (1846) and Schenk (1871, 1876) is from localities regarded as Berriasian in age. Unfortunately all but one of their original specimens are missing.

## SYSTEMATIC DESCRIPTIONS

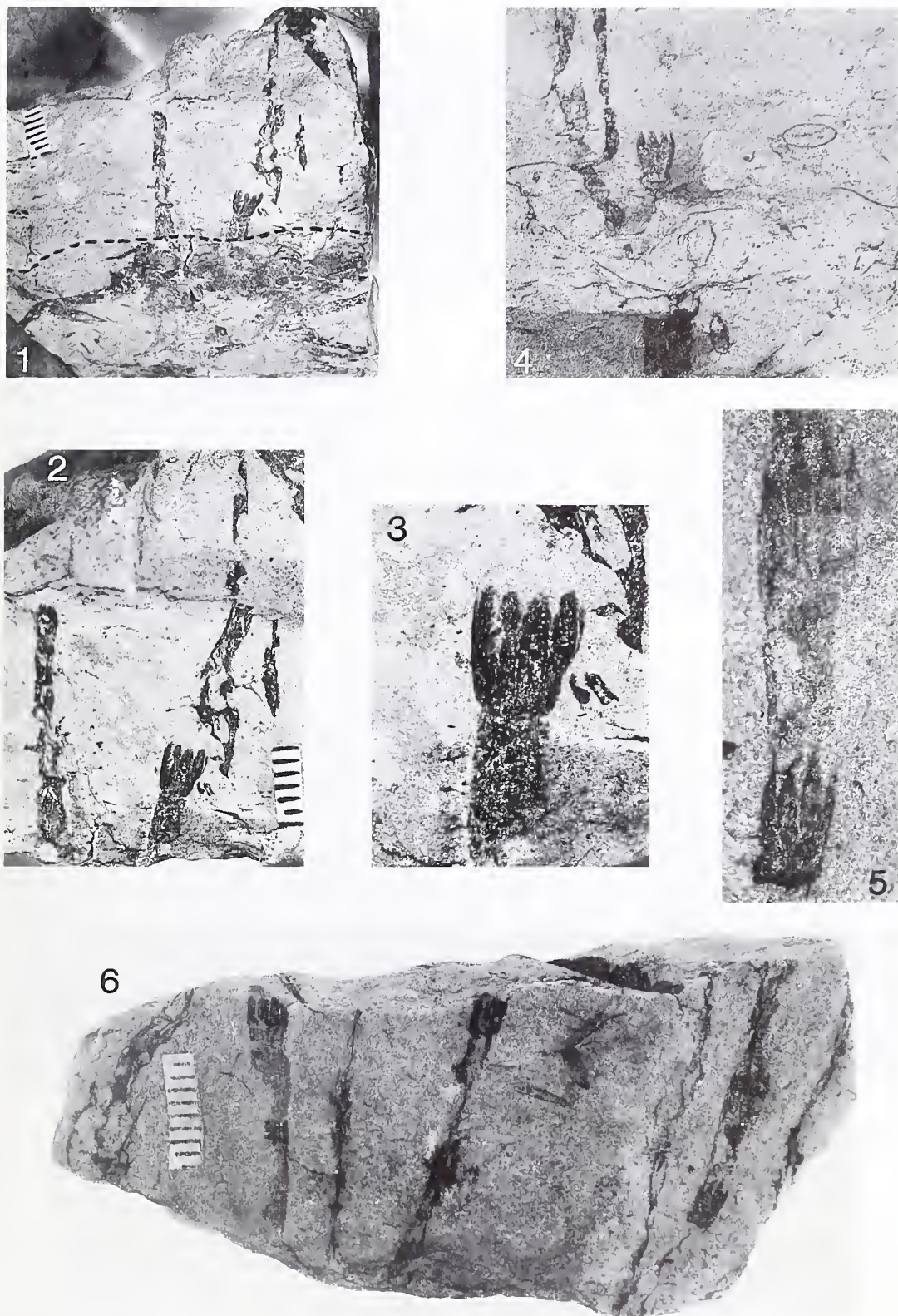
Class SPHENOPSIDA  
Order EQUISETALES  
Family EQUISETACEAE

Genus *EQUISETUM* Linnaeus

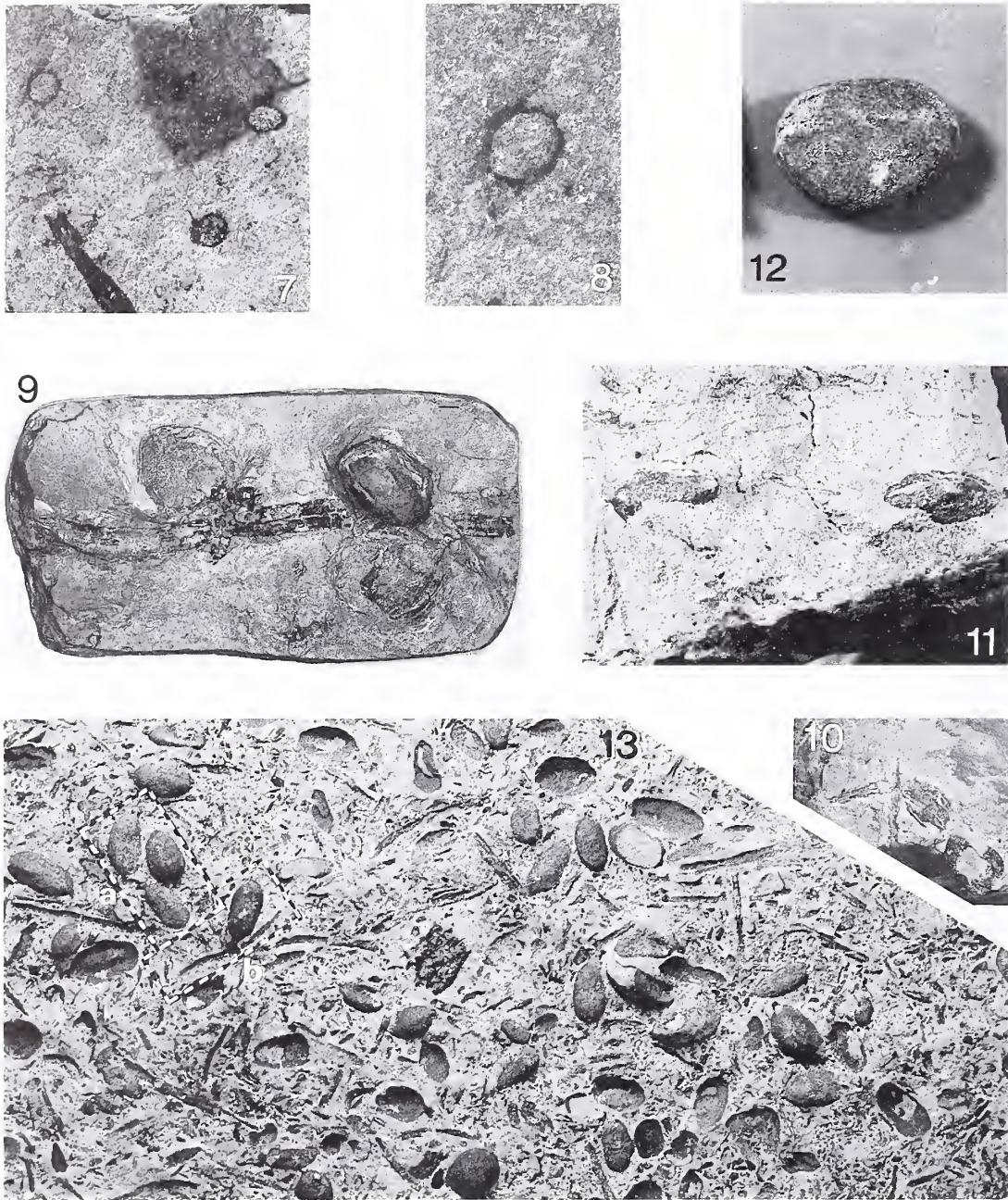
Opinions and conventions concerning the use of the Recent genus *Equisetum* L. for fossil species have swung back and forth over the past 150 years, as the synonymies of *E. burchardtii* and *E. lyellii* show. There is a strong argument for retaining *Equisetites* Sternberg for all extinct species, however closely they resemble modern forms, and in many ways we prefer this usage. However, there has been an increasing tendency in recent years (Harris 1961, Gould 1968) to include a species, whatever its geological age, in the living genus when differences cannot be demonstrated. This is of course common practice with Tertiary plants. Although anatomical details of *Equisetum burchardtii* Dunker are not available it is so similar to living species of the genus *Equisetum* (subgenus *Equisetum*) that it is difficult to imagine that any generic differences could exist. We have therefore decided to include it in *Equisetum* L., as indeed did Dunker and Schenk.

- | <i>Equisetum burchardtii</i> Dunker   | Figs 1–12, 14 |
|---|---------------|
| ?1824 <i>Carpolithus Mantellii</i> Stokes & Webb: 425; pl. 46, figs 3, 4; pl. 47, fig. 1. (Tubers only).                            |               |
| ?1827 <i>Carpolithus mantellii</i> Stokes & Webb; Mantell: 56; pl. 3, figs 3, 4; pl. 3*, fig. 1. (Repeat of Stokes & Webb figures). |               |
| ?1833 <i>Carpolithus Mantellii</i> Stokes & Webb; Mantell: 245; text-fig. on p. 246.  |               |
| 1846 <i>Equisetites (Equisetum) Burchardti</i> Dunker: 2; pl. 5, fig. 7.  |               |
| 1846 <i>Carpolithus Lindleyanus</i> Dunker: 22; pl. 2, fig. 7 in part.  |               |
| 1846 <i>Carpolithus cordatus</i> Dunker: 22; pl. 2, figs 7 (in part), 10.   |               |
| 1846 <i>Carpolithus Huttoni</i> Dunker: 22; pl. 2, fig. 8.  |               |
| 1846 <i>Carpolithus certum</i> Dunker: 22; pl. 7, fig. 3.   |               |
| 1852 <i>Equisetum Burchardti</i> Dunker; Ettingshausen: 10; pl. 1, figs 3, 4.   |               |
| 1871 <i>Equisetum Burchardti</i> Dunker; Schenk: 205; pl. 22, figs 1–5; pl. 30, fig. 1 (see Fig. 10).                               |               |
| 1876 <i>Equisetum Burchardti</i> Dunker; Schenk: 157; pl. 26, fig. 1.   |               |
| 1894 <i>Equisetites Burchardti</i> Dunker; Seward: 27; pl. 1, figs 5, 6.  |               |
| 1983 <i>Equisetum burchardtii</i> Dunker; Watson: 266; pl. 13, figs 1–3.  |               |

EMENDED DIAGNOSIS. Underground rhizomes 2–4 mm wide, internodes at least 3 cm long, each node bearing 2 or more ellipsoidal tubers up to 1.5 cm long. Vertical aerial shoots 2–3 mm wide arising at intervals from rhizome; internodes up to at least 3 cm long. Whorl of 8 leaves at each node on aerial



**Figs 1–6** *Equisetum burchardtii* Dunker. 1, small block of sediment with plants in growth position. The dotted line marks the junction between the bedding plane (below) with rhizomes and tubers and the vertical face (above) with lower parts of aerial shoots; **neotype** (here selected). Dunker Catalogue 57,  $\times 1$ . 2, vertical face of same specimen showing underground parts of aerial shoots *in situ*,  $\times 2$ . 3, single shoot showing whorl of leaves with blunt tips at node; part of same specimen,  $\times 5$ . 4, vertical face with various ramifying shoots, some of which may be vertically ascending rhizomes; Dunker Cat. 6,  $\times 2$ . 5, aerial shoot showing sharply pointed leaves in successive whorls; Dunker Cat. 7,  $\times 5$ . 6, vertical face of whole block as last, with closely spaced, well preserved underground parts of aerial shoots; see Figs 7, 8 for top surface of this block, Dunker Cat. 7,  $\times 2$ .



**Figs 7–12** *Equisetum burchardtii* Dunker. 7, 8, top horizontal surface of block shown in Fig. 6, showing hollow stems in transverse section (compare Fig. 48, p. 52); Dunker Cat. 7;  $7 \times 2$ ,  $8 \times 5$ . 9, *in situ* tubers attached to length of rhizome; V.1070,  $\times 1$ . 10, Schenk's (1871: pl. 30, fig. 1) original specimen showing tubers attached to rhizome; Dunker Cat. 88,  $\times 1$ . 11, *in situ* tubers from German Wealden; Dunker Cat. 87,  $\times 2$ . 12, typical isolated tuber from Germany, very closely similar to numerous English specimens in B.M. (N.H.) collections; Dunker Cat. 85,  $\times 2$ .

**Fig. 13** *Equisetites yokoyamae* Seward. Surface of block showing portions of rhizomes and numerous tubers, may not be in growth position; see text for discussion. The dotted lines mark the areas figured by Seward (1894): a, Seward's fig. 3; b, Seward's fig. 3\*. [N.B. Seward attributed the wrong specimen number to the former]. V.2335,  $\times 1$ .

shoot, fused laterally to form adpressed or somewhat inflated sheath up to 5 mm long. Acutely pointed leaf tips free for more than 1 mm; well-defined commissures between leaves reaching almost to node. [Internal anatomy unknown; microscopic details unknown].

NEOTYPE. Specimen 57 in the old Dunker Catalogue,

Museum für Naturkunde der Humboldt Universität, East Berlin, here selected. Figs 1–3.

TYPE LOCALITY AND HORIZON. Harrel bei Bückeberg, north-west Germany. Berriasian.

ENGLISH MATERIAL. The only English specimens so far reliably identified as *E. burchardtii* are those in the B.M.(N.H.)

collected by Rufford. They are merely recorded as being from Ecclesbourne, near Hastings, and therefore their exact horizon is in doubt. They could have come from either the Ashdown Beds Formation or the Wadhurst Clay Formation and thus may be either Berriasian or Valanginian in age. It seems most likely that they are from the Ashdown Beds as there are no other records of tuberous rhizomes from the Wadhurst Clay (Allen 1976: 428).

**DESCRIPTION.** The true identity of the specimens described as fruits by Stokes & Webb (1824) and likened to palm kernels by Mantell (1827, 1833) is not known, but they were almost certainly isolated *Equisetum* tubers of which there are many in the B.M.(N.H.) collections (Fig. 12). Such tubers attached to *Equisetum* rhizomes (Fig. 9) were not described from the English Wealden until much later (Seward 1894), when they were identified with *Equisetum burchardtii* Dunker (1846) from the Wealden of Germany, where they are known also from aerial shoots. There is no doubt about the specific identity of the material described by Seward (1894), but in the absence of the Stokes & Webb specimens we retain Dunker's specific epithet. Dunker (1846) at the same time erected a number of *Carpolithus* species, also probably isolated *Equisetum* tubers. Unfortunately none of Dunker's figured specimens have been recognized in any of the German collections, but the old Dunker collection in the Museum für Naturkunde, East Berlin, still has several excellent small blocks showing *in situ* rhizomes, tubers and aerial shoots. One of these (Figs 1–3) is here selected as the neotype for *Equisetum burchardtii*. This block has rhizomes, fine roots and tubers on the bottom horizontal face (Fig. 1, below the dotted line) and portions of aerial shoot on one of the vertical faces (above the dotted line). One of the aerial shoots (Figs 2, 3) clearly shows the details of a leaf sheath, with a whorl of probably eight leaves. This particular specimen has eroded leaf tips but other specimens (Figs 4–6) show acute, sharply pointed, intact tips. The shoots shown in Figs 5 and 6 have several successive nodes intact and therefore the internodal length has been taken from here, though of course these specimens must represent only the extreme basal portions of aerial shoots.

No microscopic details of *E. burchardtii* have been obtained. All attempts at making cuticle preparations were unsuccessful. As with *E. lyellii* the cuticle is rendered featureless by oxidative maceration. Our best hope is to obtain newly collected, naturally oxidized fragments now that several of the old German Wealden localities have been reopened (Riegel *et al.* 1986).

**DISCUSSION.** The specimen of *E. burchardtii* in Fig. 9 with thin rhizomes, long internodes and bearing tubers at the nodes is strikingly like the living species *Equisetum palustre*. The known parts of the aerial shoots may also be compared to such a species with few facets (leaves); typically five in *E. palustre* (Hyde *et al.* 1969: fig. 26) and eight in *E. burchardtii*. All the known features of *E. burchardtii* point very strongly to it being a typical species of the genus *Equisetum* subgenus *Equisetum*. All extant members of this subgenus are deciduous, with soft, easily broken aerial shoots which decay at the end of each growing season, whilst bearing food storage tubers on the rhizomes which, in all but one species, lack a central canal. The presence of tubers therefore indicates that the fossilization process began during the winter after the deciduous aerial stems had died down. Thus it is clear that the *in situ* shoots attached to tuberous rhizomes were the underground parts and of course a seasonal climate is strongly indicated,

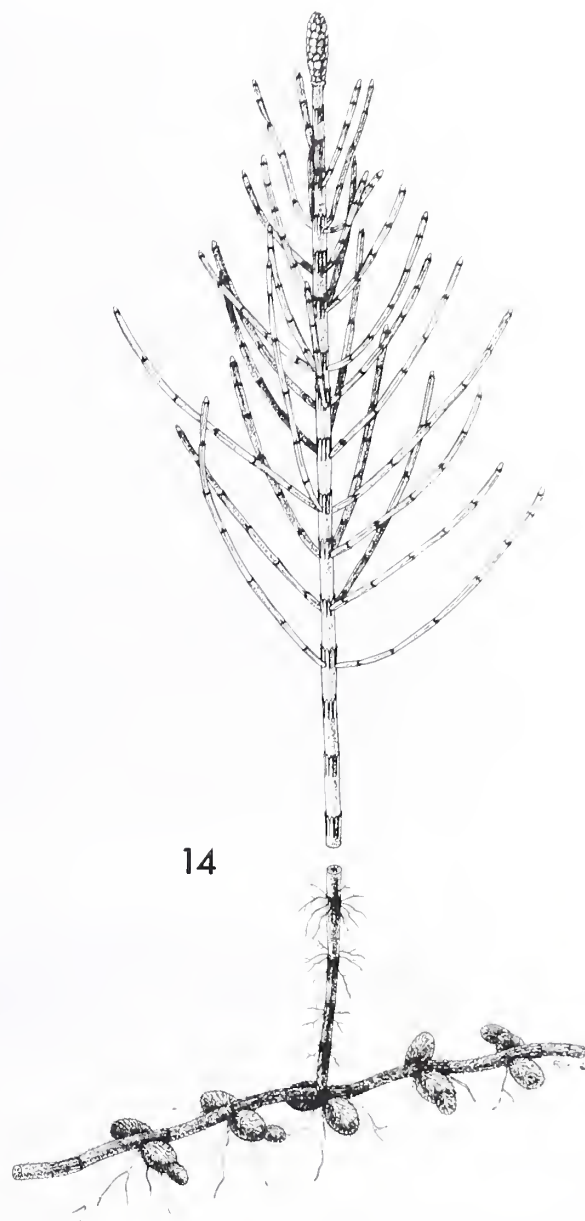


Fig. 14 Suggested reconstruction of *Equisetum burchardtii* Dunker. Approximately  $\times \frac{1}{2}$ . © Joan Watson, 1990.

supporting the conclusions of Batten (1975) and Harris (1981) from other palaeobotanical evidence, and Allen (1976) on sedimentological grounds. It seems probable that *E. burchardtii* displayed other features typical of its subgenus. In the suggested reconstruction in Fig. 14 we have incorporated some of these likely features, such as solid, strongly angular branches distinct from the main axis and cones with rounded tops. The choice of monomorphic habit with cones borne at the apices of the green shoots is purely arbitrary.

**COMPARISON.** For comparison with other tuberous rhizomes from the English Wealden see below under *Equisetites yokoyamae*, p. 42.

*Equisetum burchardtii* has been listed in several floras from different parts of the world but it is impossible to assess the reliability of the identifications. Most similar are some of the

specimens, including tuberous rhizomes, which Fontaine (1889, 1905) described from the Lower Cretaceous Potomac Group of the U.S.A., ascribing them to various species. Berry (1911) redescribed this material and transferred some of it to *E. burchardtii*, but unfortunately the whereabouts of the specimens is now unknown.

*E. burchardtii* is distinct at the subgeneric level from the Wealden species *Equisetites lyellii*, which shows significant differences from all the living species and is discussed in detail below. From what we know about *E. burchardtii* it is more similar to living members of the group than to any of the other Mesozoic species which are known in comparable detail.

### Genus *EQUISETITES* Sternberg

- 1833 *Equisetites* Sternberg: 43.  
 1894 *Equisetites* Sternberg; Seward: 23.  
 1961 *Equisetum* Linnaeus; Harris: 14.  
 1968 *Equisetum* Linnaeus; Gould: 155.

The genus *Equisetites* Sternberg was put into synonymy with *Equisetum* Linnaeus by Harris (1961), who considered that morphologically none of the fossil forms assigned to *Equisetites* could be separated at the generic level from extant *Equisetum*. This is probably true for most of the species hitherto described, but that is not to say that *Equisetites* should not be retained for use as it was originally intended, that is for plants which cannot positively be assigned to the living genus. We therefore propose its reinstatement and are retaining within it two of the Wealden species.

*Equisetites yokoyamae* Seward is so poorly characterized that it really does not warrant a name change on the basis of the information available, and *Equisetites* seems a perfect repository for it. *Equisetites lyellii* (Mantell), on the other hand, is now known in considerable detail including its anatomy. The evidence shows that the anatomical features of *E. lyellii* are rather further removed from modern *Equisetum* than the external morphology suggests, and in the light of this we prefer to retain it within *Equisetites* Sternberg.

#### *Equisetites yokoyamae* Seward Fig. 13

1894 *Equisetites Yokoyamae* Seward: 33, text-figs 2, 3.

HOLOTYPE. V.2335, B.M.(N.H.)

TYPE LOCALITY AND HORIZON. Ecclesbourne near Hastings. Berriasian or early Valanginian; see comments above about the age of *E. burchardtii* and the Ecclesbourne locality.

DESCRIPTION AND DISCUSSION. Fig. 13 shows part of the block of red-stained fine white sandstone covered with tubers and lengths of very thin rhizome, on the basis of which Seward (1894) erected the species *Equisetites yokoyamae*. The dotted lines on Fig. 13 indicate the areas figured by Seward (1894: figs 3, 3\*). Almost all the material attributed to *E. yokoyamae* by Seward is in this same matrix and could represent a single occurrence found by P. Rufford and subsequently distributed to various museums. The tubers are much smaller and narrower than most of those of *E. burchardtii* (Fig. 9) from the English Wealden but the German material (Figs 10–12) shows a wide range in variation of tuber size. Fig. 10 illustrates the sole remaining German figured specimen (Schenk

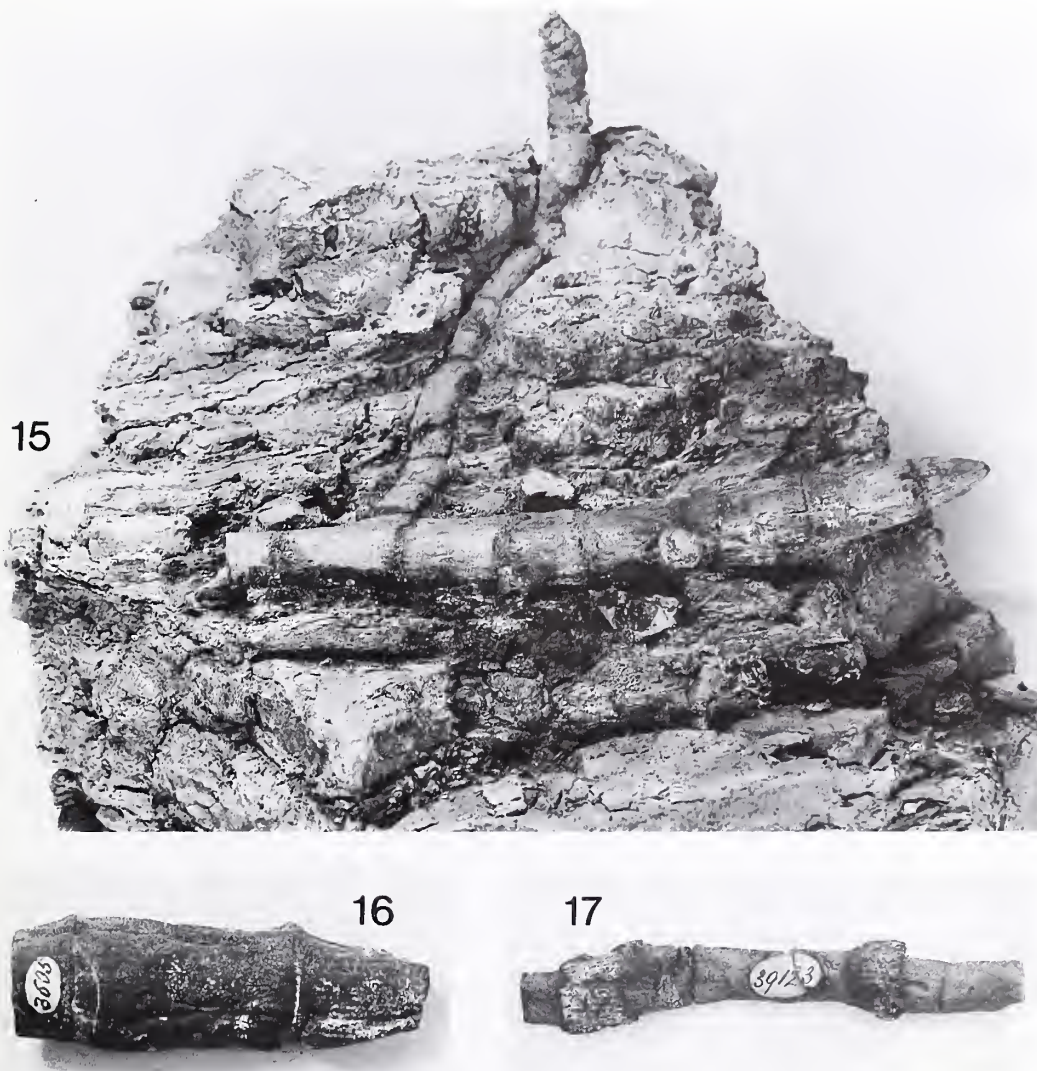
1871: pl. 30, fig. 1), which is very close in shape and size to *E. yokoyamae* and could represent the same species in a different preservational state. However there are a few other specimens in the B.M.(N.H.), tentatively attributed by Seward to *E. yokoyamae*, which have extremely small tubers and thin rhizomes (see Appendix). The extreme difference in size between these and the largest *E. burchardtii* tubers must indicate the presence of more than one species. But, in the absence of cellular detail and without information from aerial parts, the exact nature of *E. yokoyamae* remains uncertain.

Other tuberous rhizomes recorded by Allen (1976: 427) from the Weald Clay are unlikely to be either *E. burchardtii* or *E. yokoyamae*. Those from the Slinfold Soil Bed have rhizomes about 1 cm in diameter, whereas the fattest rhizomes of *E. burchardtii* barely reach 4 mm. Specimens from the Vann Lane Sand have rhizomes 1.5 cm across and the tubers are rounded rather than elongate (Allen, personal communication). It seems likely that several herbaceous, tuberous species of *Equisetum* were present in the Wealden flora.

#### *Equisetites lyellii* (Mantell) Seward Figs 15–42, 45–51, 53–55, 57–63, 67

- 1833 *Equisetum Lyellii* Mantell: 245, figs 1–3. (Rhizomes figured as aerial shoots).  
 1846 *Equisetites Phillipsii* Dunker: 2; pl. 1, fig. 2. (Poor figure of fat rhizome).  
 1871 *Equisetum Phillipsii* Dunker: Schenk (*pro parte*): 206; pl. 22, figs 6–8; *non* pl. 22, fig. 9. (Rhizomes in their fattest form).  
 1871 *Equisetum Lyelli* Mantell; Schenk: 207; pl. 22, figs 10–12. (Rhizomes of medium size).  
 1894 *Equisetites Lyelli* (Mantell) Seward: 24; pl. 1, fig. 4. (Mainly list of material in B.M.(N.H.) collections).  
 1913 *Equisetites lyelli* (Mantell); Seward: 85; pl. 11, figs 1a, 1b.  
 1941 *Equisetites lyelli* (Mantell); Allen: 362, text-figs 54–56; pl. 24. (*In situ* material with new diagnosis and full synonymy including doubtful identifications).  
 1947 *Equisetites lyelli* (Mantell); Allen: 303, text-fig. 57. (Soil beds and rhizomes showing vascular strands).  
 1983 *Equisetum lyellii* Mantell; Watson: 265; pl. 13, figs 5–8; pl. 14, figs 1–7, 9–12. (Including preliminary description of stomata and sporangiophore).

DIAGNOSIS (emended after Allen, 1941). Underground rhizomes horizontal, thick, usually unbranched, with large central canal, having internodes of variable length and width, internode length 5 mm to 3 cm or more, width less than 1 cm to over 2 cm. Hollow erect stems arising singly or in pairs with internodes typically 7 mm long and 7 mm wide in the lower subterranean part, tapering to 3 mm long and 2.5 mm wide in the upper aerial part; some nodes of aerial shoots bearing whorls of narrow branches. Central canal of aerial shoot large, surrounded by a ring of vascular bundles with crescent-shaped metaxylem, tracheid thickenings probably annular. Cortex with ring of vallicular canals, oval in section [vascular bundles and vallicular canals presumed to equal leaves in number]. Leaf sheath varying from half as long to nearly as long as internode, composed of slender tapering leaves united to near their toothed apices by commissures with strongly sculptured surface; commissures extending backwards from node. Whorls of up to 46 leaves on rhizome, 26 on the lower



**Figs 15–17** *Equisetites lyellii* (Mantell). 15, Allen's (1941) specimen of a rhizome with growing tip and aerial shoot preserved in growth position; specimen now broken, printed from original negative; K.2221,  $\times 1$ . 16, 17, the two remaining original specimens figured by Mantell (1833). 16, **lectotype** (here selected), 3605,  $\times 1$ . 17, 39123,  $\times 1$ .

and 18 on the upper parts of the erect stems. Tubers not formed.

Ordinary epidermal cells of internode in longitudinal files, rectangular with sinuous walls marked with transverse ridges; features less apparent in longer, narrower cells of leaf sheath. Broad longitudinal band of scattered stomata in lower part of each segment of leaf sheath on aerial shoot; stoma oval, typically 40  $\mu\text{m}$  long and 20  $\mu\text{m}$  wide; outer stomatal cells level with surrounding surface, ornamented with beaded sculpture along slit-like aperture and around distal margin.

Sporangiophore peltate, head circular with about 24 surface ribs radiating from centre; epidermal cells rectangular with sinuous walls parallel to ribs. Sporangia rounded [number unknown], containing spores of *Pilasporites allenii* Batten.

**LECTOTYPE.** Specimen 3605 in the B.M. (N.H.), here selected. Figured by Mantell (1833: 245, fig. 3). Fig. 16.

**TYPE LOCALITY AND HORIZON.** The locality given by Mantell (1833) as Pounceford was later confirmed by Hunter (1835)

and Topley (1875: 498) as being Poundsford, south of Burwash Common, E. Sussex (TQ 637225). Poundsford lies athwart the Purbeck–Ashdown boundary and the quarries from which the specimens apparently came were in the top Purbeck (Topley 1875: 37–41, 408), of presumed Berriasian age.

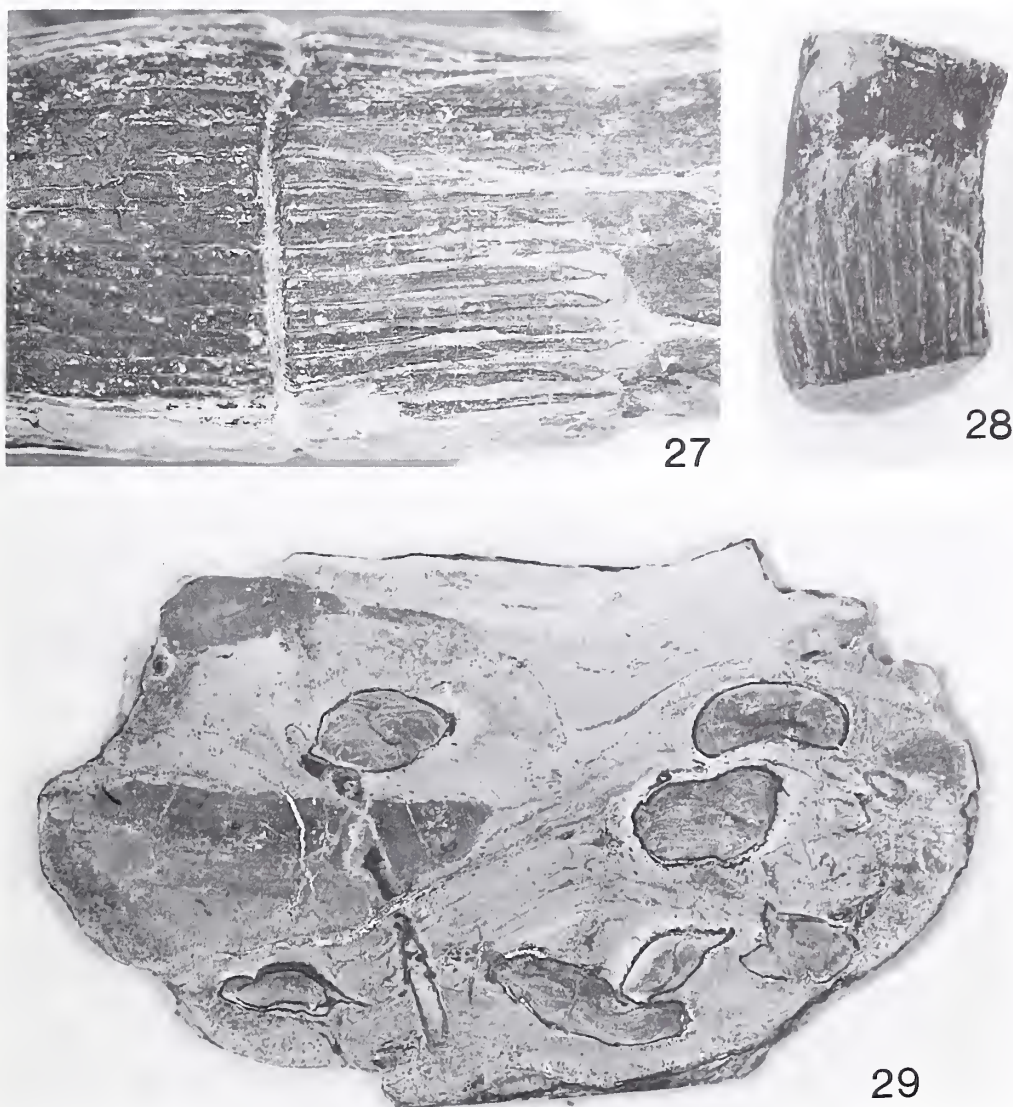
**STRATIGRAPHICAL RANGE.** The material from the type locality is the oldest recorded occurrence of *E. lyellii*. The youngest stratigraphically are specimens from the Hackenden Soil Bed within the Grinstead Clay Member of the Tunbridge Wells Sandstone Formation, in the upper part of the Hastings Bed Group.

**MATERIAL.** The material studied comes from numerous localities (see Appendix) and horizons and consists of the following parts of the plant: a large number of lengths of underground rhizome found *in situ* in various states of compression or as internal moulds; short lengths of underground parts of aerial shoots, also *in situ* and often attached to the rhizome; two separate but related finds of petrified underground parts in a carbonate matrix; presumed erect axes from above ground



**Figs 18–26** *Equisetites lyellii* (Mantell). All except Fig. 22 × 1. 18–25, rhizomes showing different preservation states and typical variation in width and internode length. 18, 19, rhizomes with well preserved leaf-sheaths and the longest internodes; 18, V.710; 19, V.59. 20, the fattest rhizome known, V.45457. 21, internal mould of hollow rhizome showing impressions of vascular strands along internodes, V.51137. 22, single node of same specimen showing apparent leaf-gaps, × 4. 23, narrow rhizome of similar preservation showing vascular bundles as ferruginous grooves (see Allen 1947: fig. 57A), K.2139. 24, shortest internodes known, probably close behind growing tip missing from right, V.63058. 25, rhizome with aerial shoot apparently emerging below node, V.28642. 26, portions of aerial shoots with well preserved leaf-sheaths and typically retaining circular section; a, V.63070; b, V.28643; c, V.63071; d, V.63072.





**Figs 27–29** *Equisetites lyellii* (Mantell). 27, portion of rhizome showing large number of leaves in whorl with pointed tips intact; V.710,  $\times 4$ . 28, portion of aerial shoot with eroded tips of leaves; V.28643,  $\times 4$ . 29, vertical cut face of carbonate nodule containing rhizomes with well preserved cellular structure; V.63059,  $\times 1$

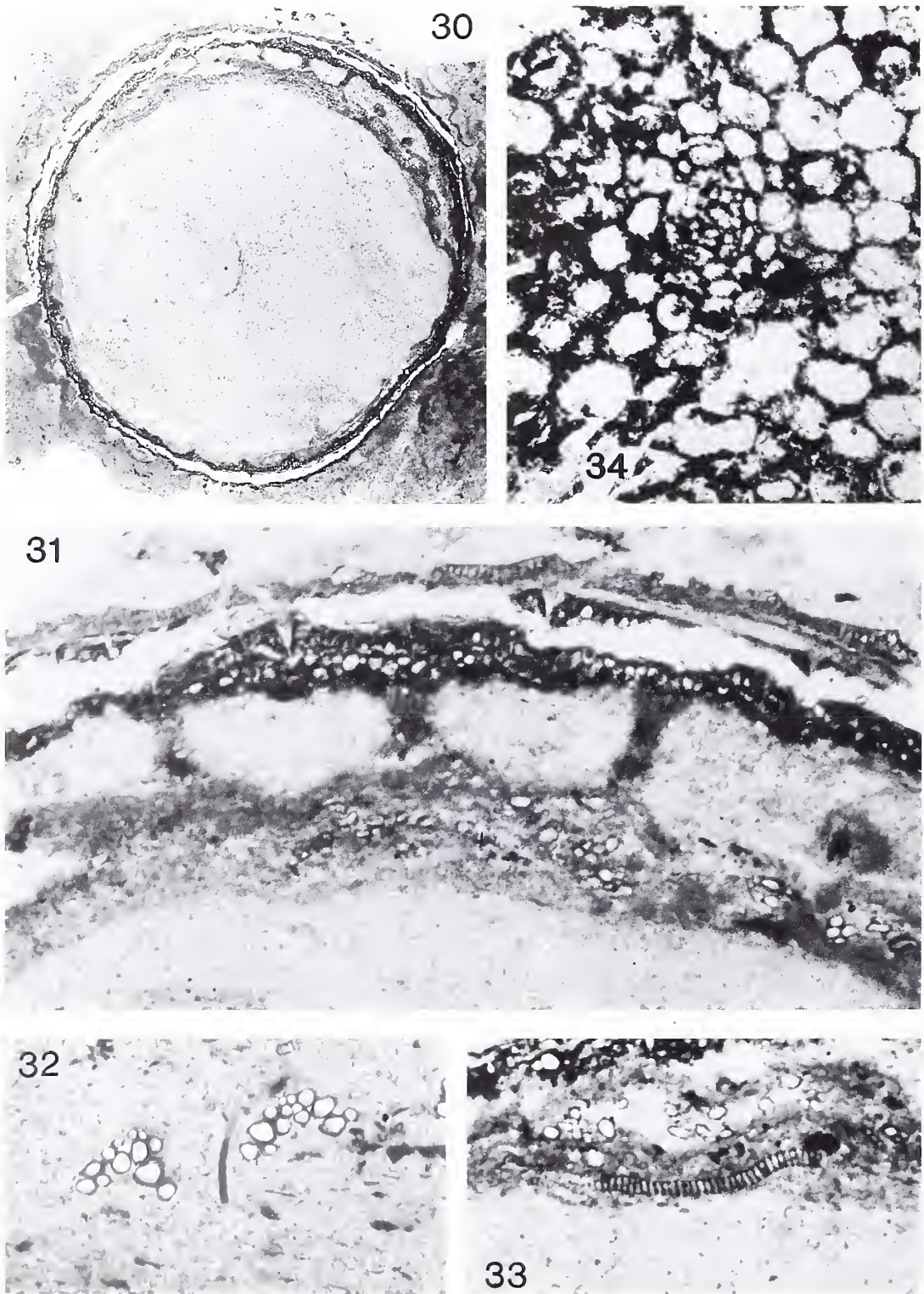
level which are known only from fragment partings in compression form; the probable spores both dispersed and from sporangiophores. Unfortunately the aerial parts are those about which we know least and organic connection has not strictly been proved. The dispersed spores are also identified only on evidence of abundant association.

All the material is from the English Wealden. *E. lyellii* is present but uncommon in the German flora.

**DESCRIPTION.** Figures 15–28 illustrate the easily recognizable and most characteristic features of *E. lyellii*: the thick horizontal rhizomes with a large central canal and a large number of leaves, up to 46 per node; the narrower upright stems also with a large number of leaves; the very short internode length of both rhizome and aerial shoot. The absence of tubers must also be regarded as diagnostic.

When Mantell (1833) first described *Equisetites lyellii* he failed to distinguish between rhizomes and aerial parts and

did not recognize that the specimens were in growth position. This was first recognized by Allen (1941). Two of Mantell's original specimens are shown in Figs 16 and 17. The former, which has been selected as the lectotype, is a clearly recognizable portion of rhizome with one whole and two half internodes, elliptical in cross section. The tip of the specimen (Fig. 16, right side) which Mantell (1833: fig. 2) figured vertically as the 'cryptogamous head' is a broken, squashed, hollow internode. Specimen 39123 (Fig. 17) is more problematical, being very poorly preserved with incrustations of heavy mineralization. On the basis of the internode length we are inclined to think that this is also a piece of rhizome, although it is at the lower limit of recorded rhizome width. However, the specimen in Fig. 23 (collected and figured by Allen, 1947: fig. 57), which is very little wider, is without doubt a portion of rhizome, though with much shorter internodes. A third specimen (3579) in the B.M.(N.H.), which has the same poor preservation, is possibly the original of Mantell's figure 1



Figs 30–34 *Equisetites lyellii* (Mantell). All sections prepared from carbonate nodules. 30, transverse section of aerial shoot indicating large central canal and vallicular canals; V.44953,  $\times 10$ . 31, portion of same section showing ridged stem surface, cells of cortex, vallicular canals and vascular bundles out of place;  $\times 50$ . 32, t.s., vascular bundles showing more extensive xylem than in living species; phloem was probably present between the arms of the V-shaped xylem; V.44951,  $\times 50$ . 33, displaced tracheid seen longitudinally, showing thickenings; V.44953,  $\times 50$ . 34, part of cortex shown in Fig. 35, with small subsidiary trace of uncertain nature, discussed on p. 49; V.44949,  $\times 400$ .

(1833), but is less easily recognizable than the other two. About a dozen other rhizomes with this same preservation survive; probably all were collected by Mantell at Poundsford. Four of them (see Appendix for details) are of particular interest in that they retain their original circular cross section. The hard, blue-grey calcareous matrix with a metallic ring which fills the rhizomes is probably one of the 'Blue limestones' of Topley (1875: 37). It seems likely that early lithification by calcium carbonate forming locally in the mud before compression produced incompressible patches. One of the four rhizomes is circular for half its length but shows considerable compression in the other half without lateral spreading (see Allen, 1947). Allen (personal communication) has observed similar partially uncompressed rhizomes in the field, associated with various lateral changes of lithology.

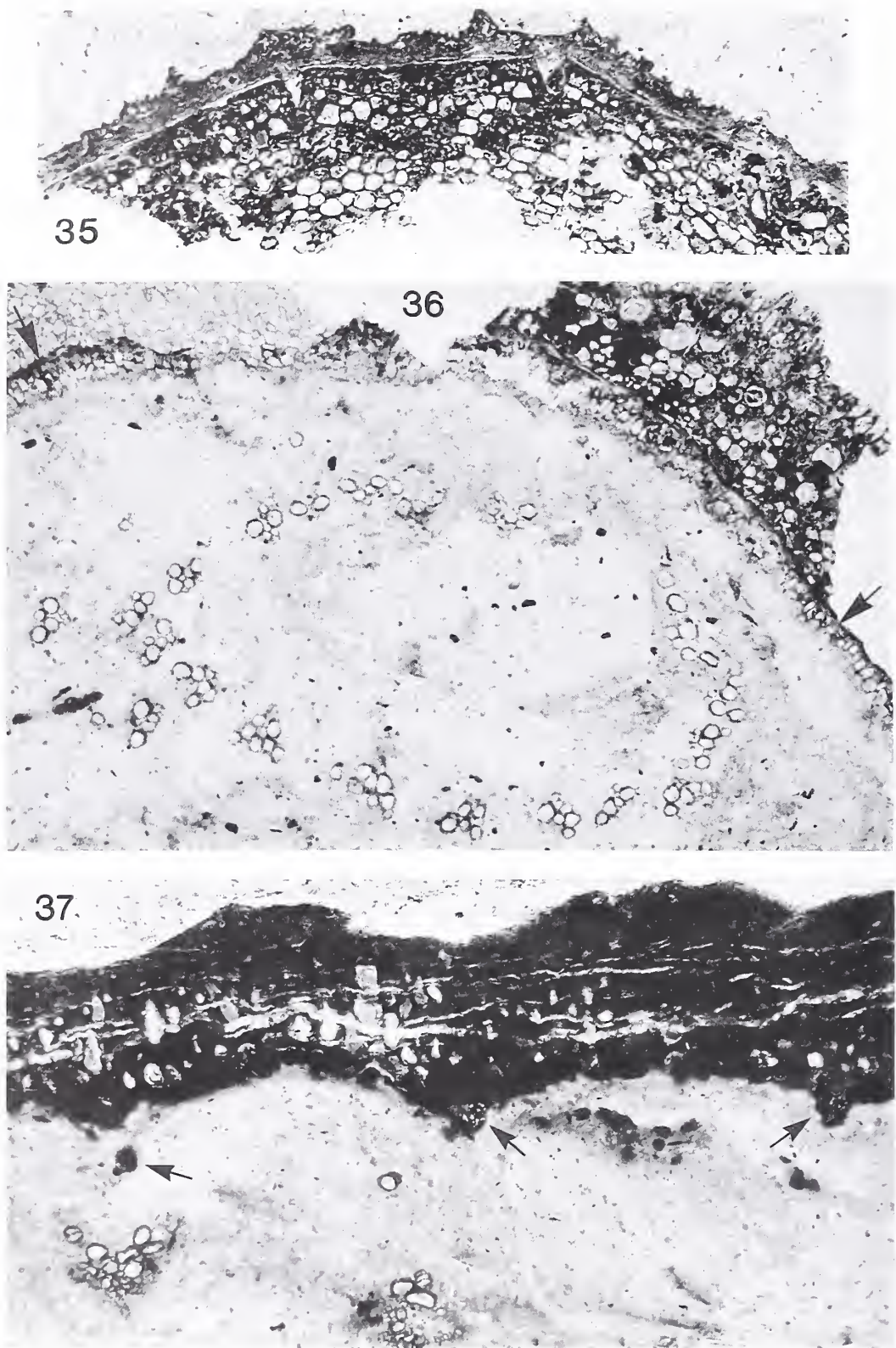
Since Mantell's time *E. lyellii* in growth position has been collected extensively by Allen, Batten and others in the numerous soil beds in the Wealden of Sussex. Material collected and studied by Allen (1941, 1947) included the splendid specimen from the Brede Soil Bed (Wadhurst Clay) illustrated in Fig. 15, which shows the rhizome complete with growing tip and an extensive length of the subterranean part of an upright stem. Unfortunately the growing tip and most of the aerial shoot are now missing from this specimen (Sedgwick Museum, K2221) and Fig. 15 has been printed from one of Allen's original glass plate negatives. Allen's description of *E. lyellii* (1941) based on the *in situ* soil bed material is very comprehensive, and apart from SEM studies of the cuticle can be little improved upon. The new information presented here comes largely from two other sources; compressions of aerial parts dispersed in the fragment beds and anatomically preserved material in carbonate nodules (Fig. 29) found by P. J. Whybrow and C. H. Shute of the B.M.(N.H.) in the Balcombe (= High Brooms) Soil Bed in the upper Wadhurst Clay near East Grinstead.

The epidermal details of the subterranean parts, which of course lack stomata, were figured by Allen (1941). Indeed cuticle preparations are easy to obtain, although they very rapidly deteriorate in acid, becoming so featureless that no cell outlines can be seen. The cells and their bars of thickening (Figs 45–49) are best seen in naturally oxidized fragments. Some of the best dispersed fragments, from the Cuckfield No. 1 borehole (Lake & Thurrell 1974), have yielded details of the stomata which were hitherto unknown. The stomata are scattered in a wide band (Fig. 40) in the flat areas of the leaf sheath between the commissures (Fig. 39). Fig. 39 shows part of a well-preserved leaf sheath from the borehole. This specimen has well-preserved stomata, two of which are shown in Figs 41 and 42. The outer stomatal cells are seen to be level with the surface and have beaded ornamentation around the perimeter and along the stomatal slit. Amongst living species we found strikingly similar stomata (Figs 43, 44) in *Equisetum sylvaticum*. It seems reasonable to suppose, therefore, that the stomata of *E. lyellii* have the same unusual construction as in living *Equisetum* (Hauke 1957, Chatterjee 1964, Page 1972a), the guard cells being completely covered and hidden by the two subsidiary cells which are seen at the surface. These are usually referred to as the 'stomatal cells'. Both the distribution and form of the stomata are features of taxonomic significance which will be further discussed below.

Figure 53 shows the freshly split surface of a block of fragment bed photographed under paraffin. Surfaces such as this have provided valuable new information about the sub-aerial parts of *E. lyellii* but have also posed problems to which

we have as yet no answers. Most prominent amongst the various dispersed remains on these blocks are the so-called nodal diaphragms (Figs 53, 55). These wheel-like bodies are familiar from almost all fossil equisetalean species (Harris 1961, Gould 1968) although no such structure is known in living species. Watson (1983) has already indicated that we have reason to call into doubt their real nature, and to suggest that they may often, if not always, be a preservational effect. During the course of this study several specimens of *Equisetum telmateia* obtained for epidermal preparations were kept in a polythene bag in a dry, centrally heated room for several months. Apart from obvious changes in colour and dryness the plants remained ostensibly intact. However, upon removal from the bag and subsequent handling, they all fell apart into single internodes with a leaf sheath at the top node and a 'nodal diaphragm' at the bottom node as shown in Fig. 56. Clearly the drying and shrinking of the hollow stem had caused it to shrivel inwards a few mm above the node whilst the node itself remained as a firm ring. This has had the effect of making the vascular bundles between the vallicular canals appear as spokes radiating from the centre, presenting an unmistakable similarity to the nodal diaphragms so well known in fossil *Equisetum*. It is easy to see that during preservational degradation this resistant structure could readily become detached and rotate through 90°, the position in which the diaphragms are commonly preserved (Harris 1961: figs 4D, 5C). The nodal diaphragms found associated with *E. lyellii* are all 2 mm or less in diameter, and are almost certainly from slender branches which are one of the least known features of this plant. Allen (1941) reported seeing only one branch, about 2 mm across, but further evidence of extensive branching in some shoots comes from the specimen shown in Fig. 50 and from a number of specimens such as that in Fig. 48. The specimen in Fig. 50 on the surface of the fragment parting appears to be an unexpanded shoot with unexpanded whorls of branches at each node. Fig. 48 is one of many branch-like fragments about 2 mm wide which are cylindrical and have epidermal cells with bars of thickening (Fig. 49) closely matching those of *E. lyellii* epidermis from elsewhere on the plant.

Other circular bodies with radiating striations (Figs 57–60) are quite different from the nodal diaphragms in having a complete covering of cuticle, and are without doubt the sporangiophores of *E. lyellii*. Some have been removed whole from the matrix using HF and then either macerated or mounted for the SEM. The outer surface seen in Fig. 61 shows that the epidermal cells are of the usual rectangular wavy-walled type and Fig. 60 shows the radiating striations as strong surface ridges. The macerated specimens yielded compact clumps of spores such as that in Fig. 62, presumably representing the contents and shape of a single sporangium. Similar spore masses are common in the fragment partings in association with isolated dispersed spores and occur in many palynological preparations. They are sometimes attached to tissues that suggest the remains of sporangiophores. We have been completely unable to ascertain or even estimate the number of sporangia borne on the under surface of the sporangiophore, which we assume had a central stalk as usual. The fairly featureless spores (Fig. 63) lacking elaters match the probable dispersed spore *Pilasporites allenii* Batten. Attempts have been made to find elaters amongst the spore masses by mounting broken, unmacerated pieces of the sporangiophores but this has so far proved unsuccessful. However, the amount of fragment bed material studied in this



Figs 35–37 *Equisetites lyellii* (Mantell). All  $\times 50$ . 35, transverse section of cortex showing outer layer with ridged surface, and parenchymatous inner layer with notches into which outer cortex protrudes; V.44949; see also Fig. 34. 36, t.s. showing solid cortex, dark endodermis (arrows) and ring of metaxylem; V.44948. 37, t.s. of specimen showing remains of vallicular canals and small subsidiary traces (arrowed); V.44951.

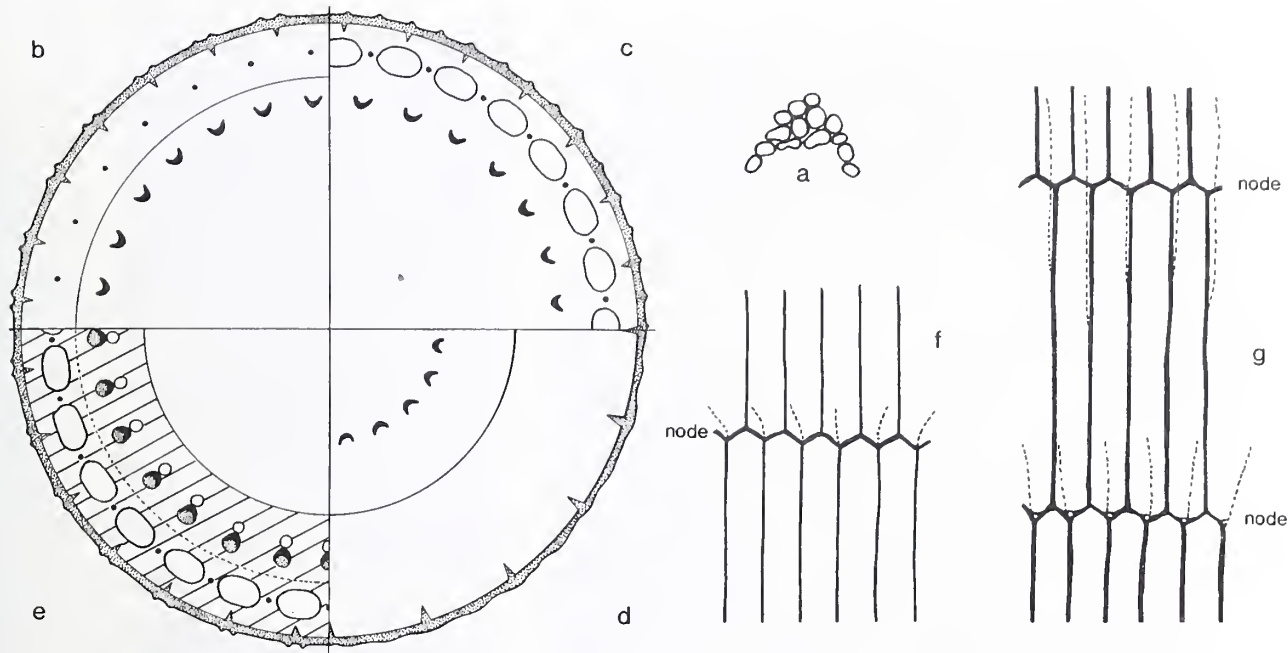


Fig. 38a–e, g *Equisetites lyellii* (Mantell). a, crescent-shaped xylem of a single well-preserved internodal bundle; protoxylem appears intact; V.44951,  $\times 50$ . b, c, d, diagrammatic transverse sections: b, V.44949; c, V.44953; d, V.44948; e, reconstructed transverse section; all  $\times 15$ . g, diagram to show suggested form of stele in *E. lyellii*; f, diagram to show form of stele in extant *Equisetum*; both  $\times 10$ .

way has been relatively limited and extensive searching of newly collected blocks might prove fruitful.

A further type of circular body (Figs 53, 54), with an even, all-over pattern of small perforations in a layer of coalified material, continues to mystify us. The diameter of these spotted bodies is about 2 mm. It seems highly likely that they originate from *E. lyellii* and any suggestions as to their nature would be welcome.

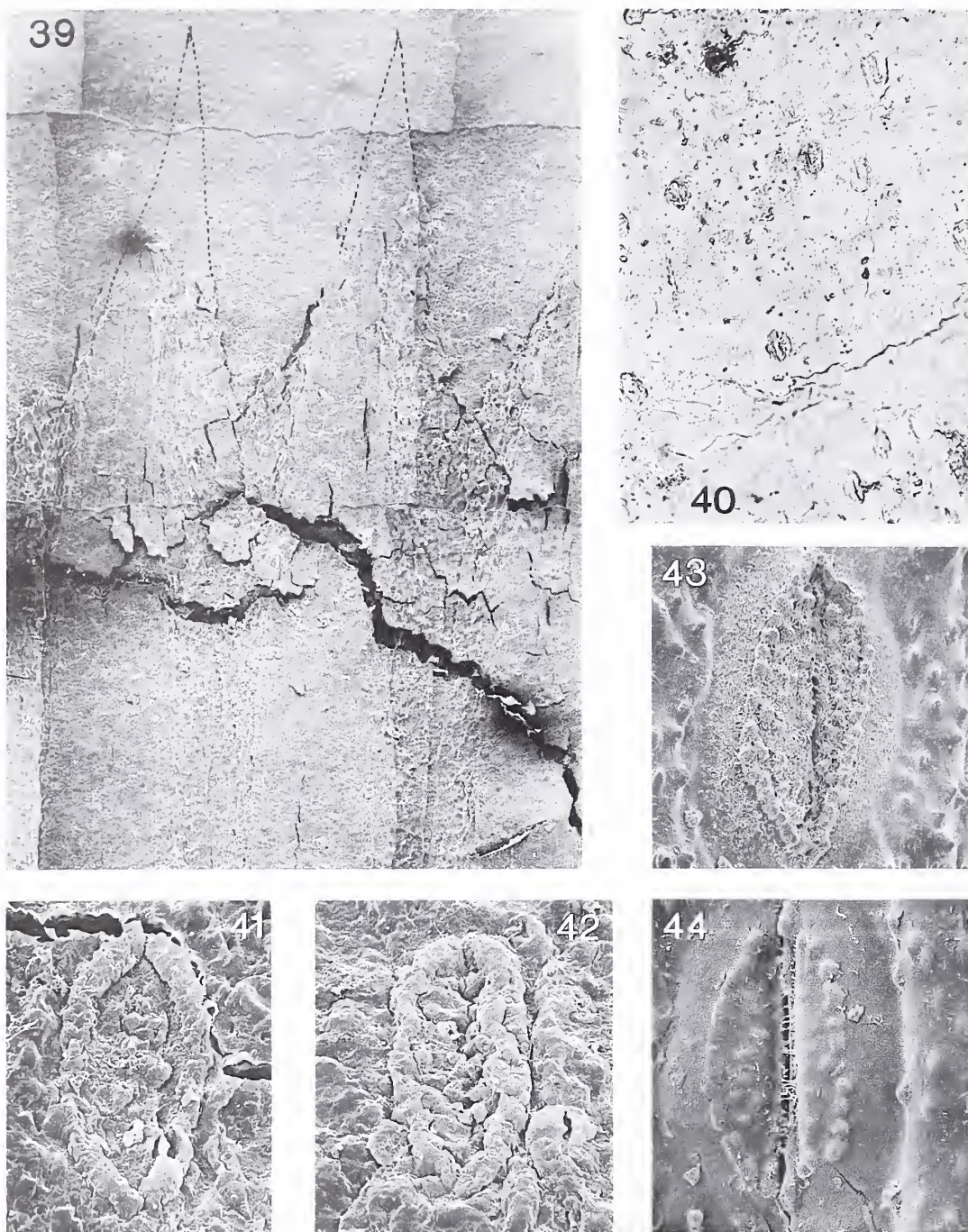
The carbonate nodule with petrified material consists of two separate finds. The first was a single nodule of calcareous mudstone, the whole of which was used to produce, by grinding, a number of longitudinal and transverse sections which were then made into permanent slide mounts. The preservation is imperfect but adds some information about the internal anatomy of *E. lyellii*. The second find of nodular material included the specimen shown in Fig. 29. This is a vertical cut-face showing transverse sections across the hollow rhizomes in growth position. Several such faces have been used to prepare cellulose acetate peels but the preservation of the plant material is less good than that in the permanent mounts. Some of the slides show little or no detail, particularly the longitudinal sections, and the information presented below has been obtained only from the transverse sections. It is certainly possible that the nodule V.63059 (Fig. 29) and others found with it would yield considerably more details of the internal anatomy with further study, but the specimens would have to be sacrificed to further cutting and extensive peeling.

Figure 30 shows the best of the transverse sections, which is obviously from an aerial shoot with a diameter of 7 mm and circular cross section. There is some doubt about whether the other sections represent rhizome or aerial shoot but certain features, such as the ridged and grooved surface (Figs 35, 38) and the number of vascular bundles, point to the latter. The rhizome surface of a living *Equisetum* undulates rather than having a sharply and evenly ridged surface like the aerial shoot of most *Equisetum* species.

The cortex is composed of two distinct layers; an outer dark, fibrous layer (Figs 31, 35) in which thickened cells are sometimes seen, and a deep inner cortex (Figs 35, 36) of large isodiametric cells with fairly thin walls. The outer cortex is approximately 0.1 mm deep except at a point opposite the vallicular canal where it protrudes into the inner cortex in a wedge shape (Figs 35, 38c). In some slides the inner cortex is solid (Figs 35, 36, 38b) whereas in others the vallicular canals are present in it (Figs 30, 31, 37, 38c). The former are taken to indicate that a parenchymatous diaphragm was present in the nodal region; the latter are internodal sections. In the sections from both regions occur what appear to be small, circular vascular traces in addition to the main vascular bundles (Figs 34, 37, 38b, c). These resistant traces are indicated by arrows in Fig. 37. To the inside of the vallicular canals a strong dark line is sometimes present (arrows in Fig. 36) in the position where one would expect the endodermis. Inside this line the soft tissues are not preserved for more than about two rows of cells (Fig. 36). Thus the xylem of the main bundles is isolated in the middle. Most of the specimens have a ring of 28 or 30 vascular bundles, with only the metaxylem preserved. Each is a crescent or V-shaped mass of about 14 tracheids with the arms pointing to the outside (Figs 32, 35). Occasionally one or two protoxylem elements remain at the point of the V. The xylem is sometimes seen longitudinally (Fig. 33) with either annular or spiral thickenings.

The specimen shown in Figs 36 and 38d is perhaps near a node at the very base of the shoot, or even on the rhizome. It bears an appendage which appears to be a small root with a central vascular strand. It also differs from most other sections in having a much smaller ring of vascular bundles, no vallicular canals and no subsidiary vascular bundles (Fig. 36). Of course close to the node one would expect some indication of the bundles joining to form the nodal ring, but there is no such indication.

Figure 38b–d comprises diagrams of three specimens in



Figs 39–42 *Equisettes lyellii* (Mantell). 39, SEM montage of leaf sheath of aerial shoot showing sculptured cells of the commissures; dotted lines indicate positions of leaf tips broken during preparation; from fragment parting, V.63060,  $\times 50$ . 40, naturally oxidized piece of internode cuticle from fragment parting showing stomata in broad band, probably internode of aerial shoot from above ground level; V.63076,  $\times 125$ . 41, 42, two of the stomata (only 5 or 6 were found) from specimen in Fig. 39;  $\times 1000$ .

Figs 43–44 *Equisetum sylvaticum* Linnaeus. Internode stomata of living species, showing silicified surface closely resembling *E. lyellii*;  $\times 1000$ .

transverse section, and a reconstructed section which is mostly based on the available information, but has added features which are purely conjectural. The exact position of the surface ridges is not clear as it appears to vary, but the arrangement in slide V.44949 (Fig. 35) is taken as typical. It should be pointed out that in living species of *Equisetum* the surface ridges are on the same radii as the vascular bundles.

In none of the sections have we been able to identify the leaf-sheath surrounding the stem. One should consider the possibility that the layer we have identified as outer cortex might in fact be the leaf sheath very closely pressed into the contours of the stem surface. This interpretation would produce sharply defined shallow notches separating broad, flat ridges opposite the vascular bundles.

DISCUSSION. One of the outstanding differences from modern horsetails is the large amount of metaxylem in *E. lyellii*, but an even more anomalous feature is the presence of the ring of small vascular traces which, as far as we can tell, are between the vallicular canals (Fig. 37) and on the same radii as the main vascular bundles. The normal arrangement of the vascular tissue in extant *Equisetum* is shown in Fig. 38f, but there is some disagreement about the exact nature of such a stele. The various viewpoints which revolve around whether the internodal bundle is a composite structure or a single unit have been summarized with great clarity by Parihar (1965). In general terms the internodal bundles may be considered to trifurcate at the node with the median strand passing out as a leaf trace. The lateral strands diverge to the left and right and unite with adjacent strands to form the alternating ring of bundles in the next internode above. In this process of splitting and reuniting, which is condensed at the node, a continuous ring of xylem is produced. The evidence we have for *E. lyellii* indicates that the vascular arrangement at the node was very similar to that in extant *Equisetum*. We know that the vascular bundles of *E. lyellii* normally alternate in successive internodes, but not invariably. Specimen V.51137 (Figs 21, 22), which is an internal mould of the hollow rhizome with ferruginous impressions of the vascular bundles, shows this non-alternation in several places. This specimen is also of special interest in apparently displaying leaf-gaps at some of its nodes (Fig. 22). The presence of leaf-gaps in living *Equisetum* is a little-known feature described originally by Browne (1939) and later in detail by Moore (1941) from several species. We also know that the whorls of leaves usually alternate at successive nodes, and although we cannot actually demonstrate that the leaves alternate with the bundles of the internodes above, the position of the probable leaf gaps (Figs 21, 22) strongly supports this. Assuming it to be so, we can only account for the small bundles by suggesting that they are leaf traces which depart from the main bundle at some distance below the node (Fig. 39g). They would thus be on the same radius as the bundle from which they arise and also the leaf above into which they would pass as the leaf trace. On the other hand the presence of the small leaf gaps seems to us at variance with this arrangement, since we assume the traces would diverge into the leaves without further disturbance to the main vascular bundles. However, we are working at the very limits of the material and at this stage we can only speculate that such anomalous leaf departure was not universally present. Alvin & Hluštký (1979) have demonstrated a similar situation in the Lower Cretaceous cheirolepidiaceous conifer *Frenelopsis alata* (K. Feistmantel), where the steles of side branches sometimes depart from below the node.

From the above evidence it is clear that the anatomical features of *E. lyellii* are rather further removed from the modern genus *Equisetum* than the external morphology suggests, and it is in the light of this that we prefer to retain it in the genus *Equisetites* Sternberg.

Amongst modern botanists there are still differences of opinion concerning the status of the genus *Equisetum* and its subdivisions. Here we need not consider more than the two major sub-groups, subgenus *Equisetum* and subgenus *Hippochaete*, which are easily distinguishable (see Page 1972a, 1974). The main features of the former, commonly called the horsetails, have been listed above under the discussion of *Equisetum burchardtii*. To these details it may be added that the stomata occur in a broad scattered band along each

furrow of the stem. The stomatal cells are level with the surface and covered in a microscopic ornamentation of silicified beading, as in the stomata of *Equisetum sylvaticum* shown in Figs 43 and 44.

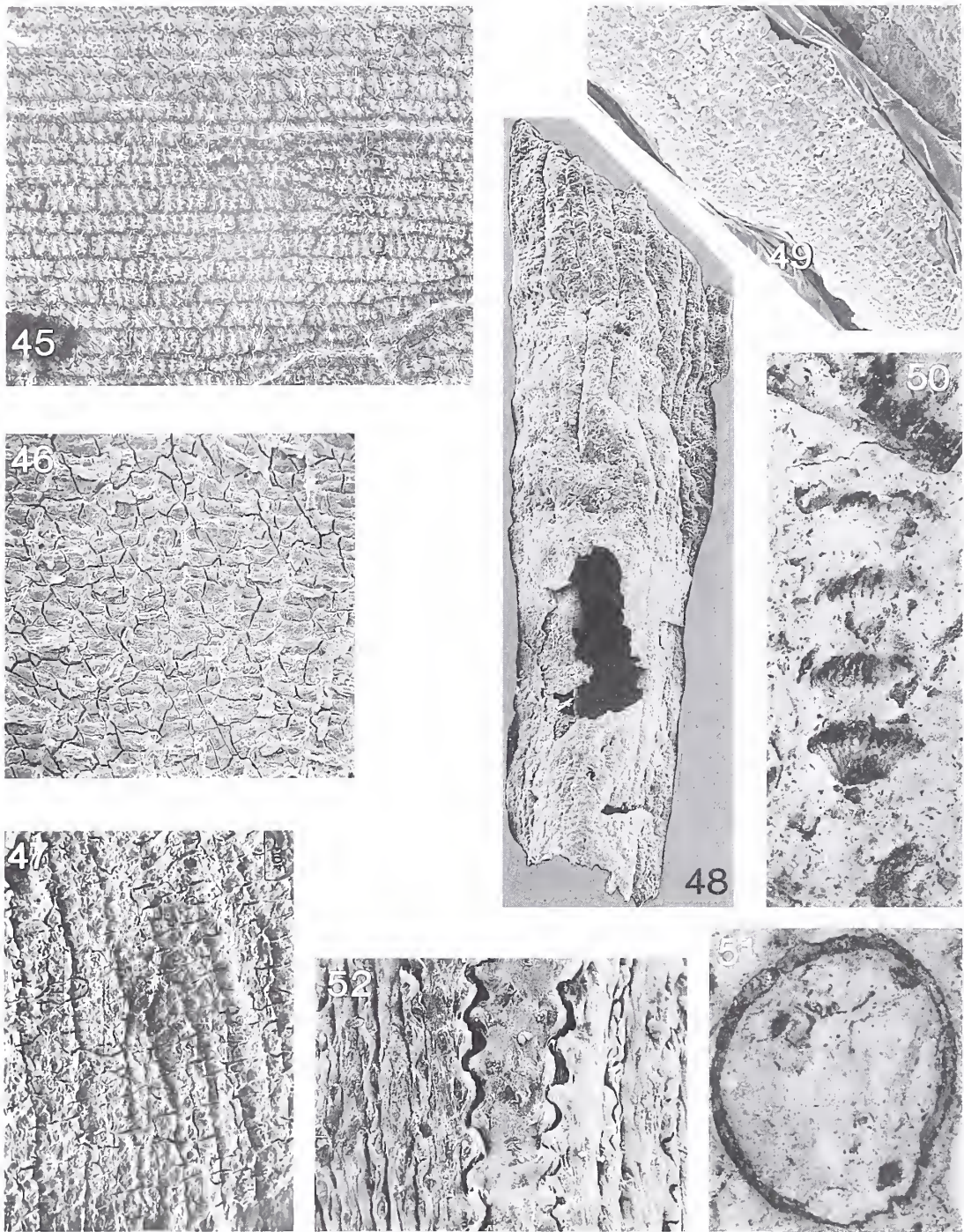
Members of the genus *Equisetum* subgenus *Hippochaete*, commonly known as the scouring rushes, are characterized by having hard, winter-green shoots which persist for up to three years. The rhizome has a large central canal and is never found with tubers. The aerial shoot has a relatively large number of leaves per node and the branches resemble the main shoot in being rounded and hollow. The stomata are arranged in one or two regular longitudinal files along the stem and are sunken in crater-like pits. The stomatal cells are non-beaded but there is coarse silica thickening around the rim of the crater (see Page 1972a).

It is quite obvious that *E. lyellii*, whilst displaying many of the features of the subgenus *Hippochaete* in its gross morphology, has stomata which both in distribution and structure are entirely typical of the subgenus *Equisetum*. Page (personal communication) considers that it should be regarded as at least subgenerically distinct from the two groups of modern species, i.e. as representing a now extinct third subgenus. Preliminary studies of the stomata of several Jurassic and Triassic species suggest that this subgenus may have been worldwide in the Mesozoic; see Page (1972b, 1974) for discussion of evolutionary evidence within the Equisetales and older articulates.

Suggested anatomical and morphological reconstructions of *Equisetites lyellii* are presented in Figs 38e and 67 respectively. The reconstructed transverse section of the aerial shoot internode (Fig. 38e) includes phloem and carinal canals which form in extant species by breakdown of the protoxylem during elongation. It seems reasonable to suppose that phloem was present between the arms of the crescent of metaxylem. The question of carinal canals is less clear as the presence of protoxylem elements in some of the bundles could be taken as an indication that these canals were absent.

The suggested reconstruction of *E. lyellii* (Fig. 67) is based on the new information given above, together with all the detailed measurements and field observations given by Allen (1941), though of necessity several features have been included for which there is absolutely no evidence. As with the reconstruction of *E. burchardtii* the choice between suggesting monomorphic or dimorphic habit was fairly, though not entirely, arbitrary. All extant members of the subgenus *Hippochaete* have only one kind of shoot but on balance we favour a dimorphic habit for *E. lyellii* for two reasons. The paucity of branches on aerial shoots in the fragment beds observed by Allen in the field (1941) must mean that many of the shoots were unbranched. The lack of a complete fertile cone but the relative abundance of isolated sporangiophores suggests that this part of the plant decayed rapidly on reaching maturity. One should also note that the sporangiophore heads of *E. lyellii* are rounded in shape, unlike modern species in which they become pentagonal as the result of close-packing. This further suggests a less robust structure, and we thus opt for the attractive notion of long, pale, fertile shoots bearing their delicate cones above the water, shedding their spores and soon becoming fragmented.

COMPARISON. Because of the exceptional material available for study this species is now known in more detail than any other Mesozoic member of the family. This makes useful comparisons even more difficult than before. The name



**Figs 45–51** *Equisetites lyellii* (Mantell). All specimens from fragment beds. 45, rhizome cuticle naturally oxidized, showing transverse bars of thickening on cells; V.63075,  $\times 100$ . 46, 47, similar pieces of cuticle in SEM; 46, inner surface, V.63060,  $\times 250$ ; 47, outer surface, V.63062,  $\times 250$ . 48, small cylinder of cuticle presumed to be a branch borne by aerial shoot; V.63063,  $\times 25$ . 49, piece of cuticle broken from middle of specimen in Fig. 48, in SEM showing cells matching those of rhizome (Figs 45, 46);  $\times 100$ . 50, probable unexpanded shoot apparently with whorls of branches; V.63967,  $\times 8$ . 51, hollow shoot broken off at surface of fragment bed; V.63064,  $\times 10$ .

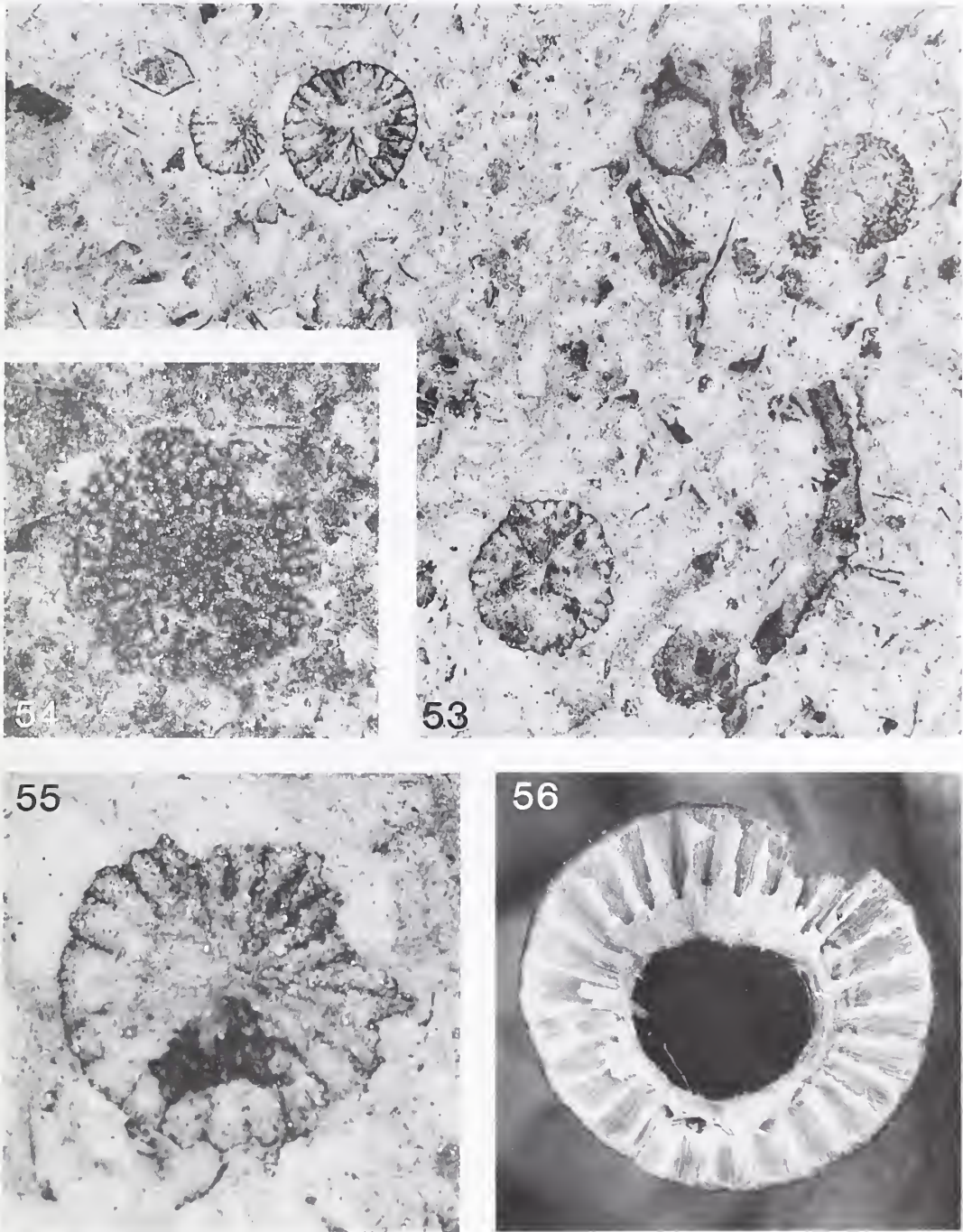
**Fig. 52** *Equisetum telmateia* Ehrhart. Desilicified internode in living species, revealing elongate, sinuous cells similar to those of *E. lyellii*;  $\times 1000$ .

*Equisetites lyellii* (Mantell) has been given to Lower Cretaceous equisetalean material from a number of countries worldwide, but at this stage it is impossible to assess the validity of these determinations. Some of them, such as the material from the Potomac Formation, U.S.A. (Fontaine

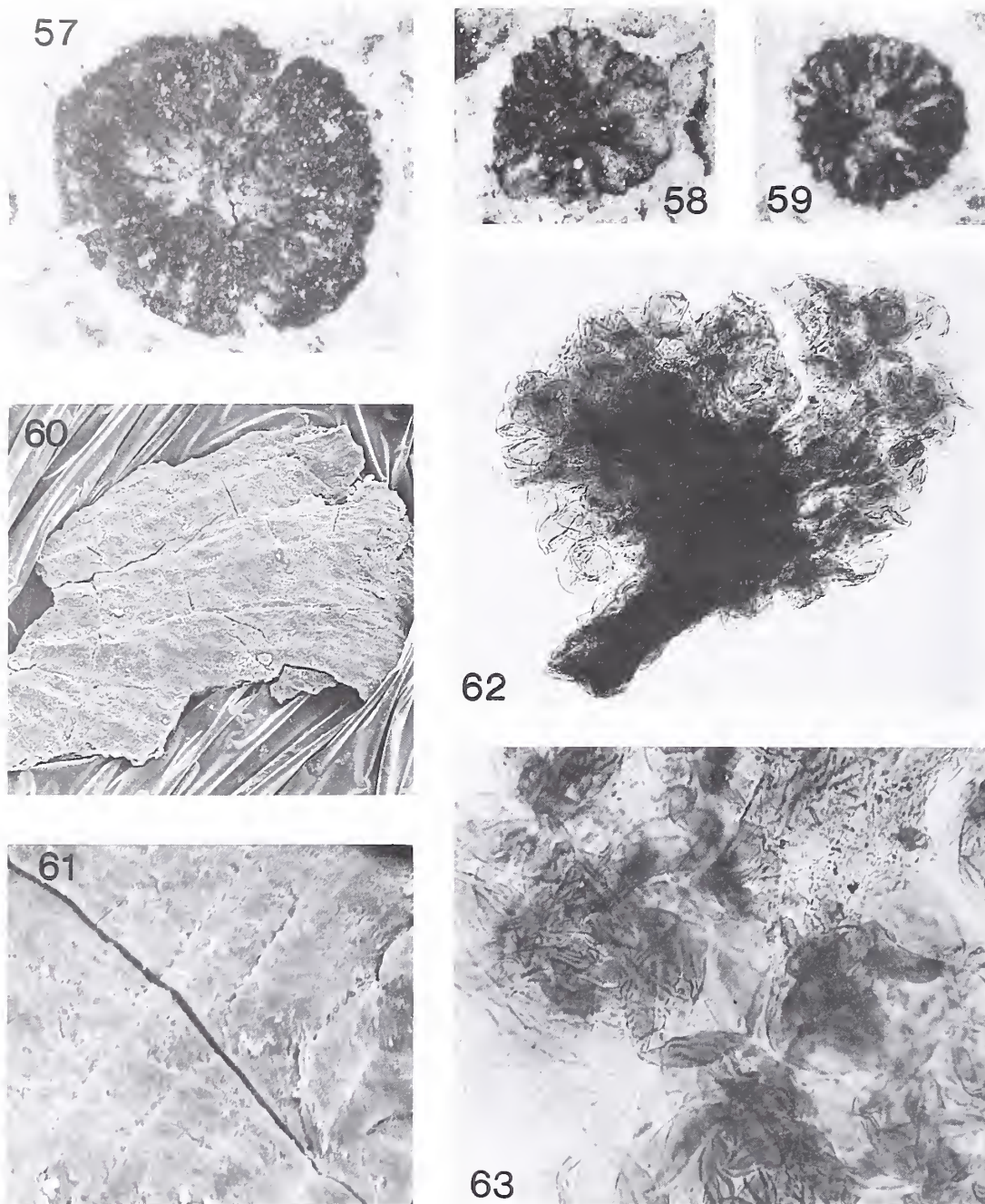
1889), are probably identical but new specimens are essential for study as Fontaine's originals are missing from the Smithsonian Institution.

The only other material known in comparable detail is that described by Gould (1968) from the Jurassic of Australia.





**Figs 53–55** *Equisetites lyellii* (Mantell). 53, typical surface of fragment bed photographed under paraffin showing nodal diaphragms etc.; V.63064,  $\times 10$ . 54, spotted disc of type very common in fragment bed, derivation unknown; V.63069,  $\times 20$ . 55, nodal diaphragm; V.63064,  $\times 20$ .  
**Fig. 56** *Equisetum telmateia* Ehrhart. 'Nodal diaphragm'; see p. 47 for discussion;  $\times 8$ .



**Figs 57–63** *Equisettes lyellii* (Mantell). 57–59, sporangiophore heads showing radiating ridges on outer surface; 57, V.63067; 58, V.63064; 59, V.63068; all  $\times 20$ . 60, unmacerated portion of sporangiophore head in SEM, curved edge on right, surface ridges radiating from broken central point on left (background, heat-damaged sellotape); V.63065,  $\times 100$ . 61, surface of same specimen showing cells with undulating walls very similar to rhizome cuticle;  $\times 500$ . 62, 63, spore mass obtained by macerating sporangiophore head, presumed to be contents of a single sporangium, V.63066; 59,  $\times 225$ ; 60,  $\times 700$ .

There are two species, *Equisetum laterale* Phillips and *Equisetum bryanii* Gould. Both are similar to *E. lyellii* in having scattered stomata and sinuous-walled epidermal cells with bars of thickening. It would be interesting to study this material again along with other Mesozoic species in the light of the phylogenetic considerations raised by the subgeneric status of *E. lyellii*.

#### SPORAE DISPERSAE

Genus *PILASPORITES* Balme & Hennelly

For remarks on *Pilasporites* see Batten, 1968.

*Pilasporites allenii* Batten

Figs 64–66

1968 *Pilasporites allenii* Batten: 638, pl.123, figs 1–4, 6, 10–14.

DESCRIPTION. For the diagnosis and fully illustrated account of this species see Batten's (1968) original description. Figs 64–66, p. 56, are representative photomicrographs of these isolated dispersed spores.

The spores of *Pilasporites allenii* were spherical or subspherical in shape before being compressed in sediment. They consist of a comparatively thick exine (exospore) surrounded by a flimsy, crumpled, closely adhering perine (perispore) which commonly bears a surface deposit of scattered granules. Despite its fragile appearance the outer membrane is clearly tough and resistant to chemical treatment, including oxidation. The exine is unornamented and devoid of a trilete or monolete aperture (Figs 63–65). In these respects the spores are entirely comparable to those of extant *Equisetum* (see for example Gullvåg 1968, Lugardon 1970, Guérin *et al.* 1972, Good 1975, Tryon & Tryon 1982, Kurmann & Taylor 1984).

Despite the alete appearance, a darkened patch is displayed on some specimens (Figs 64, 65) which resembles the 'stopper' found by Lugardon (1970) in the wall of spores of extant *Equisetum maximum*, but its diameter is more than three times as great. In this respect it suggests a closer relationship to the proximal area of geologically older spores with diminutive triradiate marks that are referred to *Calamospora*. If it did function as an operculum, which is unlikely, then the mode of germination of the spores of Cretaceous *Equisetites* may have varied, because others clearly had a tendency to split, as commonly seen in acetolysed products of extant species. Where opened in this way the exine along the margins is often slightly folded inwards.

DISCUSSION. Acetolysis, a chemical method frequently used for preparing modern and Quaternary palynomorphs for examination by transmitted light microscopy, is known to dissolve the elaters of extant *Equisetum* spores which, when coiled, envelop the perispore. No Wealden specimens have yet been found with these extra-perinous elements. The possibility that they were removed during sediment diagenesis or by chemical treatment of rock samples in the laboratory has been mentioned previously by Batten (1968). He also suggested that they might not have had them in the first place. Similar spores were reported by Gould (1968) from cones of the Australian Jurassic species identified as *E. laterale* Phillips. These also lack elaters, as do specimens isolated much earlier by Halle (1908) from compressions of *Equisetites* and those encountered in cones found more recently by Vozenin-Serra & Laroche (1974, 1976).

The pre-Quaternary fossil record of vascular plant spores with elaters is limited to associations with some Carboniferous calamites (Wilson 1943, 1963, Baxter & Leisman 1967, Good & Taylor 1974, 1975, Good 1975, 1977) and with two equisetaleans, from the Middle Jurassic (Harris 1978) and early Tertiary (Chandler 1964). Sphenophyllalean products are quite different (Taylor 1986). The calamite spores are trilete with three distally attached elaters; they are not closely similar to those of modern *Equisetum*, which are alete and have four elaters. They are thought likely to represent the most mature and best preserved specimens, whereas contemporaneous cones that yield spores lacking elaters are considered to be immature (Good 1975, 1977). Although a triradiate mark is typically present on calamite spores (Hartung 1933) its presence does not necessarily distinguish them from those of the Equisetaceae. Both Carboniferous and early Mesozoic equisetalean species have yielded spores of similar character (see for example Halle 1908 and Gastaldo 1981).

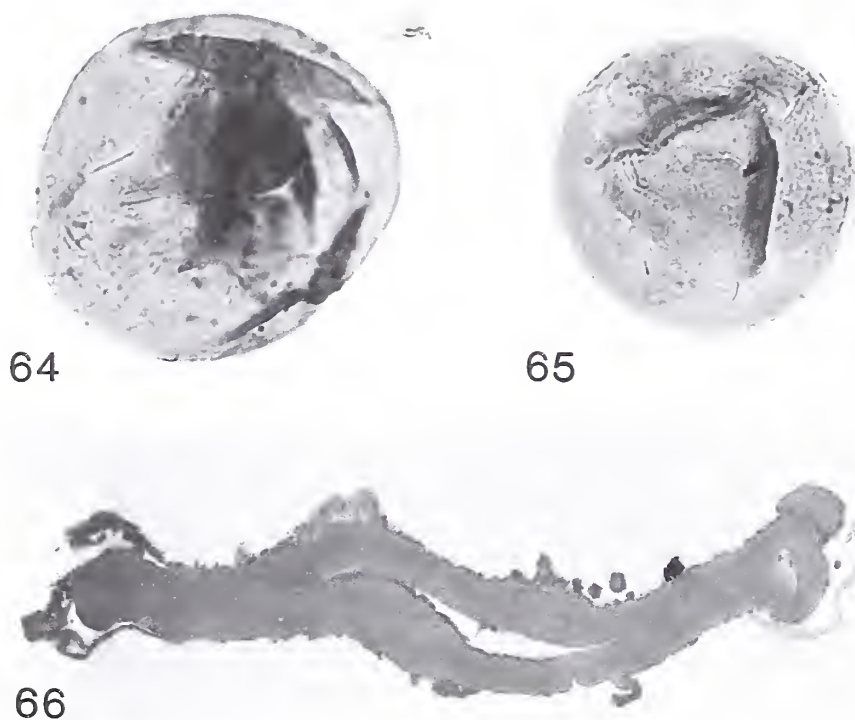
Harris (1978) found some round palynomorphs in rock matrix between sporangiophore heads of *Equisetum columnare* which seemed to bear fine threads resembling elaters. But he was not sure that they were produced by *E. columnare*, and he also noted that the threads visible on the two specimens he illustrated (Harris 1978: text-fig. 2D) were incomplete. By contrast the early Tertiary spores recovered from an *Equisetum* cone by Chandler (1964: plate 1, figs 3, 4) are remarkably similar to extant forms.

Did the spores of *Equisetites lyellii* bear elaters? If they did then surely one should find them preserved within the spore masses? Those remains of broken and decayed fertile cones which have been isolated from fragment partings without chemical treatment have so far failed to reveal any. Is this because they were immature at the time they were deposited (cf. Good 1975)? Hence, is the absence of elaters on specimens in masses a function of developmental factors, and on single and presumed fully mature spores because they decayed rapidly after dispersal? Or has the search proved fruitless because they were never developed? Species of *Equisetum* which produced elater-less spores could represent part of an extinct taxonomic grouping within the Equisetaceae, as suggested already on the basis of the morphology and anatomy of *E. lyellii*.

COMPARISON. Batten (1968, 1973) compared *Pilasporites allenii* with a number of dispersed miospores that had been referred previously to the Equisetaceae and with morphologically similar species which had not been linked to this family. Several additional records that fall into one or other of these categories are considered below.

Maljavkina (1956) referred triradiate spores she recovered from the Cretaceous of the eastern Gobi depression to a new, but invalid and superfluous, genus *Equisetacites*. Alete species included in different genera erected earlier by the same author (Maljavkina 1949) have also been linked by some Soviet palynologists to *Equisetites* or the Equisetaceae. Vinogradova (1971) described as new a palynomorph from the Jurassic of Mangyshlak and western Turkmenia which she named *Equisetites variabilis* (see also Bolkhovitina & Fokina 1971). McKellar (1974) erected *Perodolites rugosus* for Jurassic spores from the Surat Basin of Australia; these appear to be similar to *Pilasporites allenii* but have a more rigid exine and lack the dark patch seen on some Wealden forms.

Burger (1976) identified *Concentrisporites hallei* (Nilsson) Wall from the Lower Cretaceous of the Great Artesian Basin of Queensland, Australia. This species was originally reported (as *Equisetosporites hallei*) from Rhaetian and early Jurassic rocks of Sweden and considered closely comparable to, if not identical with, the spores of *Equisetites* (*Equisetostachys suecicus* (Nathorst) Halle (see Nilsson 1958: 66–67 and Batten 1968: 241). Similar, indeed probably identical, forms have been recorded from the Jurassic of France (Danzé-Corsin & Laveine 1963), Canada (Pocock 1970, referred to *Concentrisporites pseudosulcatus* (Danzé-Corsin & Laveine) Pocock) and Australia (Reiser & Williams 1969, identified as *Perinopollenites elatoides* Couper). More recently Taugourdeau-Lantz & Dubois (1979) described as new *Pilasporites petri* and *P. calabrensis* from the Middle Jurassic of Calabria, Italy. Both were considered to have probable equisetalean origins, whereas the spores referred to ?*Equisetum* by Mamezar (1986) are unlikely to have any connection with this group. Finally, a scanning electron micrograph of the surface of an inaperturate palynomorph, thought by



**Figs 64–66** *Pilasporites allenii* Batten, the probable dispersed spore of *Equisetites lyellii* (Mantell). 64, 65, V.63073,  $\times 1000$ . 64, spore showing subcircular patch of thickened exine and scattered granules on closely-adhering perine. 65, typical specimen of *P. allenii* with membranous perine closely enveloping and crumpled against the exine. 66, cross section of spore showing thick, homogeneous exine surrounded by a thin perine bearing scattered granular bodies; V.63074,  $\times 4000$ .

Kedves (1979) to have possible algal origins and identified as *Psophosphaera intrapunctata* (Kedves) Kedves, displays the sort of crumpling and scattered granular bodies that characterize the perine of *Pilasporites allenii* (compare Batten 1973: pl. 42, figs 10, 11 with Kedves 1979: pl. 3, fig. 1). None of these palynomorphs is, however, unequivocally identical with the Wealden spores.

## PALAEOENVIRONMENTAL SIGNIFICANCE

Where *Equisetites lyellii* is preserved in position of growth it is typically associated with thinly interbedded mudstones and siltstones. The latter commonly occur in lenticular units within the finer-grained deposits, forming the 'passage beds' of Allen (1959, 1976). These are subaqueous sedimentary accumulations and, although conveniently referred to as 'soil beds' for descriptive purposes, are generally not regarded as palaeosols *sensu stricto*. Allen, however, regards them as fossil aquatic soils at the 'wet end' of a continuous spectrum of soils, all supporting plants, from totally wet through reed-swamp and marsh to subaerial (1976 and personal communication). Well stratified weathering profiles indicating subaerial soils have been confirmed in the Wealden of northern France (Meyer 1976), but only suspected in southern England (Lake & Thurrell 1974, Allen 1976, 1981, Stewart 1981) where high rates of deposition and frequent erosion appear to have hindered their development. Red-mottled silts and clays with traces of roots in growth position and indications of iron-

pan development in places imply fluctuating water tables, soil-forming alterations and local leaching, but exposure does not seem to have been long enough for weathering to have completed the pedogenic process.

All the *Equisetites lyellii* soil beds were probably under water to a depth of up to 0.5 m, if not permanently then at least more often than not. Possibly the plants could have withstood total immersion for short periods. The presence of only a few widely scattered stomata on the lower parts of the stems supports an aquatic habitat. By contrast, *Equisetum burchardtii* may have grown in better-drained sediment more often exposed or above the water table. This is suggested by its occurrence in sandier facies and by the presence of tubers on the rhizomes of the plant. In extant species of *Equisetum*, these are formed and consumed on a seasonal basis but it is possible that in *E. burchardtii* this happened in response to alternating wet and dry periods. Seasons need not be invoked. Tubers characterize only those members of the subgenus *Equisetum* which grow on dry land and have deciduous aerial parts. It follows, therefore, that the Wealden species was probably a herbaceous perennial which might well have died when its habitat became swampy or permanently flooded.

For *Equisetites lyellii* the combination of a subtropical climate and the preferred habitat being standing water suggests that, despite fluctuations in rainfall (Allen 1976, 1981, Sladen & Batten 1984), die-back occurred only sporadically during periods of drought and was not an annual event. This is consistent with the 'winter-green' interpretation of the species suggested and discussed here.

The plants are visualized as occupying extensive areas of the watery late Purbeck and Wadhurst mud-plains where



Fig. 67 A suggested reconstruction of *Equisetites lyellii* (Mantell) as discussed in the text. Approximately  $\times \frac{1}{2}$ . © Joan Watson, 1990.

deposition took place slowly in quiet conditions. Some (e.g. the Brede Soil Bed) were clearly 'reed-swamp' communities fringing the shores of lakes and bays (Allen 1959). The rhizomatous system of growth enabled communities not only to spread rapidly and keep pace with changes in water depth but also prevented mud from smothering them by keeping up with sedimentation. The scattered occurrences of *E. lyellii* in other Wealden deposits (e.g. the Grinstead Clay) and the tendency for their stems and rhizomes to be more slender

may reflect a response to conditions that were less conducive to colonization and vigorous growth. These probably included slightly raised salinities.

The arenaceous units of the Wealden succession, whether interpreted as mainly representing sandy braidplains (Allen 1976, 1977, 1981) or, as previously invoked, deltaic accumulations on a large or small scale (e.g. Allen 1959, 1962, 1976, 1977, Lake 1977, Worsam 1977), were clearly inhospitable to *Equisetites* and *Equisetum*. Recent work on the distribution of dinoflagellate cysts and other algae (Batten 1982, 1985 and in preparation; Harding 1986) suggests that the Wadhurst waters were generally fresher than those of Grinstead and Weald Clay times. This could account for the scarcity of equisetalean remains in the younger formations which otherwise represent deposition in broadly similar mud-plain conditions. It could also confirm earlier suggestions (e.g. Allen 1959, Allen *et al.* 1973, Batten 1968, 1975, 1977) that the plants grew only where the water was usually fresh and hence provide an answer to the question—what killed off the established communities?

It is difficult to follow their upward development. Erect stems are commonly terminated by fragment partings, which suggests that the plants were destroyed catastrophically. Although it is possible that they could have been overwhelmed by a sudden influx of a large amount of sediment, there is generally no evidence for this. Even if it could be demonstrated, attempts by the plants to grow up through the overburden would surely be preserved. Allen (1938, 1959) found some evidence for this but it has not been proved beyond doubt. Rhizomes of modern *Equisetum* are able to grow upwards and continue above ground as aerial stems and have been found as much as fifteen feet (4.5 m) below ground in an evenly soft substrate, attached to the upper layers by thin vertical rhizomes. The fragment partings may indicate physical damage to communities (Allen 1947, 1959, Batten 1968) or sometimes merely consist of partly decomposed litter of old stems. Total destruction is not necessarily implied. Nevertheless this did take place, and the prime cause is likely to have been inundation with saline water. Complete immersion by fresh water for an extended period (years rather than months) is also a possibility. The former interpretation is supported by evidence from the ostracod and molluscan assemblages (e.g. Allen 1959, 1976, Allen *et al.* 1973, Anderson *et al.* 1967) and phytoplankton (Batten in preparation) recovered from beds that lack *E. lyellii*. Once the plants had died the stems broke off and sediment dropped into the hollow open ends, thus enhancing their chances of being preserved *in situ*.

**ACKNOWLEDGEMENTS.** During the long time this paper has been in preparation many people have assisted us and we thank them all most warmly. We are particularly indebted to Dr C. N. Page of the Royal Botanic Garden, Edinburgh, who put at our disposal his specialist knowledge of *Equisetum* with great enthusiasm. We thank Mr Richard Hartley who has skilfully brought our reconstructions to life. To Professor Perce Allen who has been most generous with material and information and has waited longer than anyone we offer our special thanks. We hope that his patience has now been rewarded.

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## APPENDIX: STRATIGRAPHIC OCCURRENCES

Details of specimens figured in this paper and other notable material not figured here.

Figure	Collection	Spec.No.	Locality	Horizon	Comments
<i>Equisetum burchardtii</i>					
1, 2, 3	Humboldt	57	Harrel bei Bückebug	Berriasian	Neotype. Figd Watson 1983: pl. 13, fig. 1
4	"	6	"	"	Figd Watson 1983: pl. 13, fig. 2
5, 6, 7, 8	"	7	"	"	"
9	B.M.(N.H.)	V.1070	Prob. Ecclesbourne, nr Hastings, E. Sussex	?Ashdown Beds	Figd Watson 1983: pl. 13, fig. 3
10	Humboldt	88	Harrel bei Bückebug	Berriasian	Figd Schenk 1871: pl. 30, fig. 1
11	"	87	"	"	"
12	"	85	"	"	"
unfigured	B.M.(N.H.)	V.1070a	Ecclesbourne, E. Sussex	?Ashdown Beds	"
"	"	V.2730b	"	"	Rufford Colln.
"	Humboldt	1984/745	Harrel bei Bückebug	Berriasian	Nice erect stems.
<i>Equisetites yokoyamae</i>					
13	B.M.(N.H.)	V.2335	Ecclesbourne, E. Sussex	?Ashdown Beds	Figd Seward 1894: fig. 3 (with incorrect specimen number) and fig. 3*
unfigured	"	V.2834	Bexhill, E. Sussex	"	Very small tubers and thin rhizomes discussed in text, p. 42.
<i>Equisetites lyellii</i>					
15	Sedgwick	K.2221	Brede, E. Sussex	Wadhurst Clay, Brede Soil Bed	Figd Allen 1941: pl. 24A; Watson 1983: pl. 13, fig. 4.
16	B.M.(N.H.)	3605	Poundsford, E. Sussex	top Purbeck	Lectotype. Figd Mantell 1833: 245, fig. 3.
17	"	39123	"	"	Figd Mantell 1833: 245, fig. 2.
18, 27	"	V.710	St Leonards, E. Sussex	Ashdown Beds	Very well preserved epidermis.
19	"	V.59	"	"	Figd Seward 1894: pl. 1, fig. 4.

Figure	Collection	Spec.No.	Locality	Horizon	Comments
<i>Equisettes lyellii</i> , cont.					
20	B.M.(N.H.)	V.45457	SE Ashurst Wood, E. Grinstead, W. Sussex TQ 412367	Wadhurst Clay, Balcombe Soil Bed	Coll. C.H. Shute & P. J. Whybrow.
21, 22	"	V.51137	"	"	Thickest known rhizome.
23	Sedgwick	K.2139	Baldslow Wood, Westfield, E. Sussex.	Wadhurst Clay, Brede Soil Bed	Figd Allen 1947: fig. 57A.
24	B.M.(N.H.)	V.63058	East Grinstead, W. Sussex. TQ 377387	Wadhurst Clay, High Brooms Soil Bed	Coll. C. H. Shute
25, 26, 28	"	26a, V.63070 26b, V.28643 26c, V.63071 26d, V.63072	High Brooms Brick & Tile Co. pit, Nr Tunbridge Wells, Kent. TQ 417594	Wadhurst Clay, High Brooms Soil Bed	Coll. J. E. Owen
29	"	V.63059	¼ mile S of Ashurst Wood, W. Sussex TQ 419364	Wadhurst Clay, High Brooms Soil Bed	Coll. C. H. Shute & P.J. Whybrow.
30-38 + other unfigd specs.	"	V.44948 <i>et seq.</i> , see Figs	"	"	Coll. P. J. Whybrow. Slides made from nodule.
39, 41, 42	"	V.63060	Cuckfield No. 1 Borehole	Wadhurst Clay	42 figd Watson 1983: pl. 14, fig. 12
40	"	V.63076	Danehill, W. Sussex TQ 382266	"	Figd Watson 1983: pl. 14, fig. 11
45	"	V.63075	"	"	Figd Watson 1983: pl. 14, fig. 2
46	"	V.63060	Cuckfield No. 1 Borehole	"	Figd Watson 1983: pl. 14, fig. 3
47	"	V.63062	"	"	"
48, 49	"	V.63063	"	"	"
50, 57	"	V.63067	East Grinstead, W. Sussex. TQ 377387	Wadhurst Clay, frag. parting above High Brooms Soil Bed	50 figd Watson 1983: pl. 14, fig. 4
51, 53, 55, 58	"	V.63064	"	"	53 figd Watson 1983: pl. 14, fig. 5.
54	"	V.63069	"	"	"
59	"	V.63068	"	"	Figd Watson 1983: pl. 14, fig. 6.
60, 61	"	V.63065	Cuckfield No. 1 Borehole	Wadhurst Clay	61 figd Watson 1983: pl. 14, fig. 9.
62, 63	"	V.63066	"	"	63 figd Watson 1983: pl. 14, fig. 10.
64, 65	"	V.63073	Danehill, W. Sussex	"	"
66	"	V.63074	"	"	"
unfigured	"	3599	prob. Poundsford, E. Sussex	? top Purbeck	Mantell Colln. Rhizomes perfectly circular in cross section
"	"	38375	"	"	"
"	"	10837	"	"	"
"	"	38375	"	"	"
"	"	V.60511	SE Ashurst Wood, W. Sussex	Wadhurst Clay	Longest rhizome spec. in Museum collns, 23 cm long with 16 internodes.